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BIOLOGICAL BULLETIN

THE BREATHING AND FEEDING MECHANISM OF THE LAMPREYS.[1]

JEAN DAWSON.

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The present study of the respiratory mechanism of the lampreys was undertaken at the suggestion of Professor Jacob Reighard and has been carried out under his direction. Preserved material of *Petromyzon marinus* Linnæus, *Petromyzon marinus unicolor* (De Kay) and *Lampetra wilderi* Gage has been examined, but these three species have been found to be so nearly alike in the structure of their respiratory mechanism that the following anatomical description of *Petromyzon marinus* holds good in all essentials for the other two species. Where measurements are given they are taken from *P. marinus* and refer to individuals of average size. The close relation between feeding and breathing in the lamprey has made it necessary to consider the mechanisms of the two together. There is without doubt a similar close relation between the mechanism of respiration and that of circulation but this has not been included in the scope of the present paper.

I. STRUCTURES INVOLVED IN BREATHING AND FEEDING.

Food entering the funnel-shaped cavity of the oral hood passes thence at the apex of the oral hood into the mouth cavity

[1] Contributions from the Zoölogical Laboratory of the University of Michigan, No. 92.

(Fig. 1, *b*). From the mouth cavity it passes through a constriction into the larger so-called pharyngeal cavity (*d*). From the pharyngeal cavity food enters the alimentary canal proper by way of the slender œsophagus (*p*) while water may conceivably enter the much larger water tube (*s*). The latter lies ventral to the œsophagus, extends caudad to the pericardial cavity, and there ends blind. Should water enter it from the pharynx it could then pour through the seven openings on each side into the gill sacs, from which it could reach the exterior by the seven external branchial openings on each side of the body (Fig. 5, *h*).

The opening from the pharynx into the water tube is guarded by a pair of velar valves (Fig. 1, *l*; Fig. 13, *l*), while valves guard also the external branchial openings (Fig. 13, *c*, *b*). Muscles control the opening between mouth cavity and pharynx and between pharynx and œsophagus. In order to understand the mechanism of these parts, each must be considered in greater detail.

A. *Oral Funnel, Mouth Cavity and Tongue.* — The oral funnel opens upon the ventral side of the anterior part of the head. In the specimens examined the average diameter of its external opening is 3.5 cm., while its dorsal opening, where it becomes continuous with the mouth cavity, has a diameter of 1 cm. Around the smaller opening of the funnel, on the boundary between it and the mouth cavity, is a supporting ring of cartilage, called the annular cartilage (Fig. 1, *t*). Attached to this cartilage and forming the muscular walls of the funnel is a three-layered muscle, the annularis (Fig 1, *u*). Fürbringer (1875) reports that the outer and middle layers of the annularis serve to attach the animal by the oral funnel while the inner layer causes the walls of the funnel to expand and contract, and this, together with the simultaneous closing of the mouth opening (opening between the oral funnel and mouth cavity), gives the animal power to suck blood or tissue which it has succeeded in rasping from its prey. The walls of the funnel become thin abruptly at their external edge, and there bear a thick fringe of rather short tentacles (Figs. 1, *i*; Fig. 2, *i*).

The posterior wall of the funnel forms with the ventral wall of the mouth cavity an angle of almost 90 degrees; the anterior

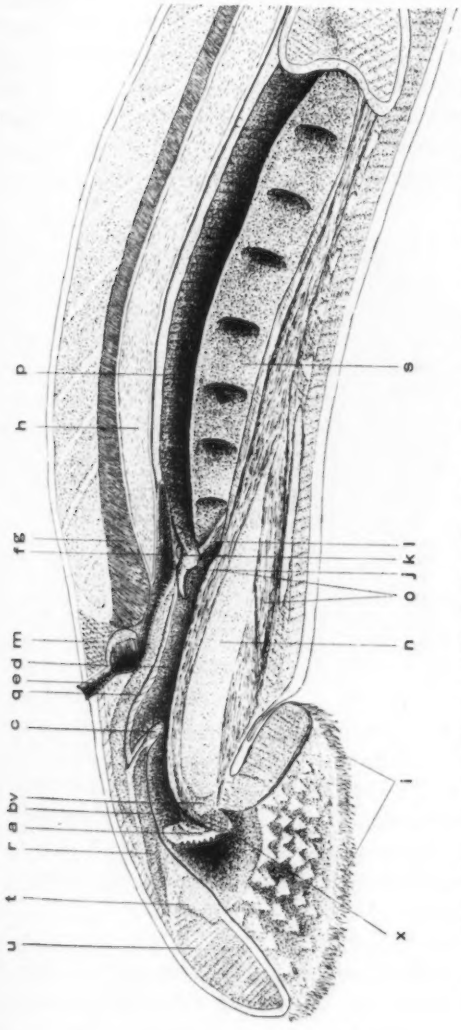

FIG. 1. Median longitudinal section through the head of *P. marinus*. *a*, tongue; *b*, mouth cavity; *c*, semiannularis muscle; *d*, pharynx; *e*, nasal tube; *f*, nasal cœcum; *g*, brain; *h*, notochord; *i*, buccal fringe; *j*, velar jaw; *k*, posterior pharyngeus muscle; *l*, velar valve; *m*, connective tissue surrounding the epiphysis; *n*, lingual cartilage; *o*, muscles of tongue; *p*, œsophagus; *q*, ethmoid cartilage; *r*, semiannularis cartilage; *s*, water tube; *t*, annular cartilage; *u*, annularis muscle; *v*, central cartilage of the tongue; *x*, anterior lobe of the tongue.

wall meets the dorsal walls of the mouth in a much gentler curve.

The funnel is lined with thick mucous membrane bearing sharp conical teeth (Fig. 2). The teeth are arranged in a series of concentric loops, the crossed ends of which lie in the anterior portion of the funnel (Figs. 1 and 2). The result of this arrangement is that any radius drawn from the center of the mouth opening strikes at least two teeth except over the posterior one fourth of the circumference of the funnel. This posterior one fourth of the funnel has teeth approximately on radii running from that portion on the central loop which has an arc of the smallest

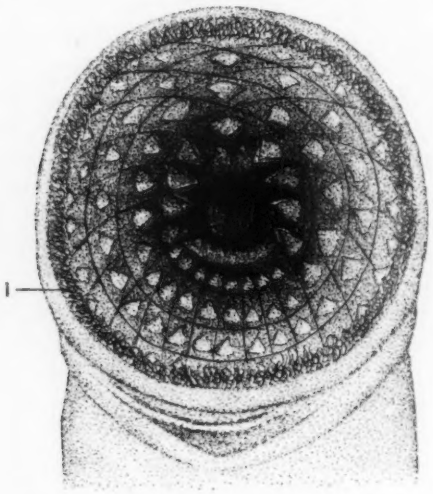

FIG. 2. Mouth of *P. marinus* showing the arrangement of the teeth in concentric loops.

radius. This is a necessary result of the geometric relation of the concentric loops (Figs. 2 and 3). The teeth on the central loop are so crowded that there are as many as on the larger outer loop. These teeth are also larger and are grown together in plates of two and more.

The end of the tongue (Fig. 1, Fig. 5 and Fig. 6) has two lateral lobes (*a*) which are covered with smooth mucous membrane and an anterior lobe (*x*) covered with plates of sharp teeth. This free end of the tongue may be seen projecting for 1 or 2 mm. into the caudal end of the funnel and the teeth on its ante-

rior lobe are thus brought into the same plane as the central teeth of the funnel and function with them in rasping. The great freedom of movement of the end of the tongue necessary in rasping is attained by its central cartilage (Fig. 1, *v*) being attached by a sort of socket joint to the enlarged anterior end of the large lingual cartilage (Fig. 1, *n*).

The mouth cavity is short and curved, about five times as long as it is wide at its middle, and extends from the oral funnel to the pharynx, a distance of about 2 cm. Its anterior end, where it meets the funnel, is larger than in any other part. Its roof and

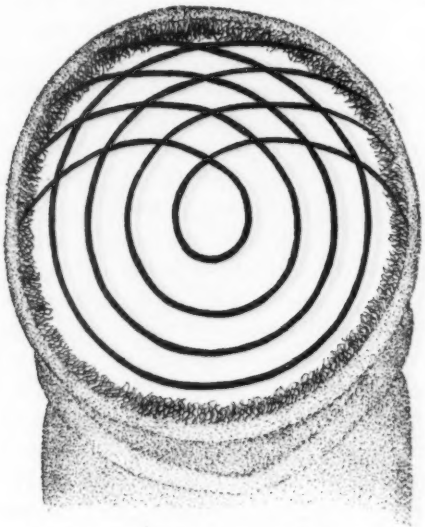

FIG. 3. Diagram of the arrangement of the teeth in the oral funnel of *P. marinus*. The heavy lines show the loops upon which the teeth are inserted.

sides are dome shaped and are formed by the semiannularis cartilage in front and by the semiannularis muscle behind (Fig. 1, *r*, *c*). The muscle arises from the posterior border of the cartilage and forms a very small portion of the roof of the mouth. The posterior portion of the dome formed by the semiannularis muscle arches so close to the ventral wall of the mouth that it greatly constricts the cavity in this region and when it contracts, completely shuts off the mouth cavity from the pharynx. The floor

of the mouth is formed by the large underlying tongue muscle (Fig. 1, *o*). The tongue as a whole is a large, long cone which stretches from the mouth opening to the ventral anterior portion of the pericardium to which it is attached by its apex. Thus the tongue underlies the whole mouth cavity, pharynx, and water tube. When the tongue is pushed forward so that its lobes occupy the flaring anterior part of the mouth cavity, its lateral lobes fall apart (Figs. 5, 6) and there is left between them a passage-way which connects the cavity of the oral funnel and that of the mouth. This passage-way, which then has a cross section equal to that of the mouth cavity at its middle, diminishes rapidly in diameter as the tongue is drawn back into the narrower part of the mouth cavity until at last it is completely closed before the tongue has reached the posterior end of the semiannularis cartilage. The end of the tongue is thus seen to act as a piston working with a short stroke back and forth in the mouth cavity, the walls of which form the cylinder while the free end of the tongue forms the piston-head and its lateral lobes the valves.

B. *Pharynx.* — Passing out of the mouth cavity through the small opening ventral to the semiannularis muscle, the food enters the cavity of the pharynx. This cavity is somewhat irregular (Fig. 1, *d*). Its dorsal anterior portion is wedge-shaped in longitudinal section and extends forward over the semiannularis muscle and semiannularis cartilage. This portion of the pharyngeal cavity thus lies dorsal to the posterior portion of the mouth cavity. The remainder of the pharyngeal cavity is about 2.5 cm. in length from where it joins the mouth cavity to where it opens into the œsophagus and water tube. Instead of having a wall whose mucous membrane lies directly upon the tongue muscles on the ventral side and against the cartilage on the dorsal side, as in the case of the mouth cavity, there is, in the wall of the pharyngeal cavity, a thin layer of muscular tissue, the pharyngeus muscle intervening between the mucous membrane and the outer layers of muscle or cartilage. The pharyngeus (Fig. 4, *c*), which is fully described by Fürbringer (1875), entirely envelops the pharyngeal cavity and ends on a raphe on the mid-ventral line of the cavity. It is in contact with the mucous membrane except in the ventral lateral part of the

pharynx. Here between the pharyngeus muscle and the mucous lining of the cavity on its lateral walls are stretched two muscles, the hyomandibulari-semiannularis and the hyomandibulari-glossus. These muscles cause the mucous membrane to project

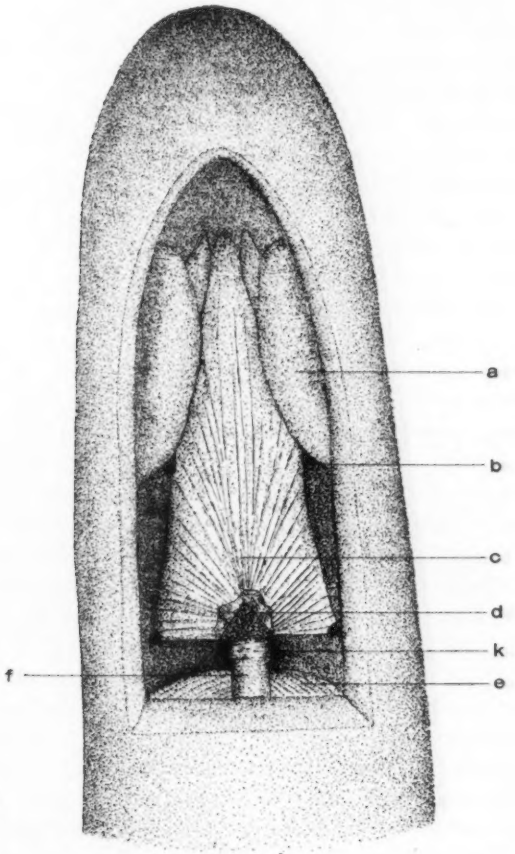

FIG. 4. Dorsal side of the head of *P. marinus* dissected to show the muscles overlying the pharynx and œsophagus. *a*, basilaris muscle; *b*, supporting cartilage; *c*, pharyngeus muscle; *d*, raphe of pharyngeus muscle; *e*, gill sac; *f*, œsophagus; *k*, posterior pharyngeus.

into the cavity in the form of a longitudinal ridge on each side.

The position of these muscles explains the difference between the size of the pharyngeus muscle viewed from the dorsal side (Fig. 4) and the actual size of the pharyngeal cavity (Figs. 1 and 5).

The outer supporting walls of the pharyngeal cavity outside of the pharyngeal muscle are: on the ventral side, the large tongue muscle; on the dorsal side, the ethmoid cartilage; on the anterior one half of the lateral walls, the basilaris muscle which expands and contracts the anterior half of pharyngeal cavity; lying dorsal to the basilaris muscles are found the large salivary glands which when the muscles act cause, according to Fürbringer (1875), a great flow of saliva.

The posterior pharyngeus is a strong bundle of muscular fibers arching over the mouth of the œsophagus between the walls of the nasal canal and that of the œsophagus (Fig. 1, *k*, and Fig. 4, *k*). This muscle lies just posterior to the pharyngeus muscle and when contracted closes off the œsophagus completely from the pharynx. When food reaches the posterior part of the pharynx, this muscle must relax to allow the food to pass on its way to the intestine.

The mucous membrane on the dorsal wall of the pharynx is continuous with that on the dorsal wall of the œsophagus, while that on the ventral wall is continuous with that on the ventral wall of the water tube. The ventral wall of the œsophagus and the dorsal wall of the water tube begin where the pharynx ends and continue caudad in close contact, parallel with the long axis of the body, to where the water tube ends, just anterior to the pericardium (Fig. 1). At the extreme anterior edge of the united walls of the pharynx and water tube there projects forward a pair of jaws which, on account of their connection with the velar valves, may be called velar jaws (Fig. 1, *j*; Fig. 5, *j*; and Fig. 6, *j*). They extend into the posterior part of the pharyngeal cavity and look like the jaws of a beetle. So close is the resemblance that at first sight one easily imagines that the animal has by some means swallowed a beetle, the jaws of which are lying in the pharynx. In Fig. 4, these jaws would lie beneath the triangular raphe (*d*).

The jaws are smooth and glossy and are covered with mucous membrane. Each is thick at the base where it unites with the

other and quite rapidly tapers to its point. The space between the jaws when they are open is a broad but incomplete ellipse; when closed, the points of the jaws come together forming an entire but narrower ellipse.

The jaws extend forward from the free end of the united walls

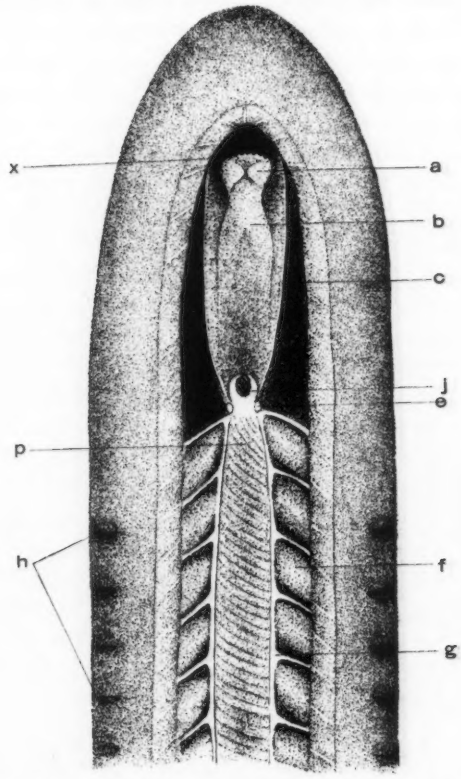

FIG. 5. Dorsal view of the head of *P. marinus* dissected so as to expose the cavities of the pharynx and œsophagus. *a*, lateral tongue lobe; *b*, tongue; *c*, pharyngeus muscle; *j*, velar jaws; *e*, posterior pharyngeus; *f*, gill sac; *g*, gill pouch; *h*, external branchipore; *p*, œsophagus; *x*, anterior lobe of the tongue.

of the water tube and œsophagus and in the same plane so that the greater part of their bulk lies ventral to the œsophagus. The position is not clearly shown in Fig. 1. The plane of the jaws is moreover oblique to the long axis of the pharynx which dips

ventrad to join the œsophagus and water tube. It results that the jaws extend obliquely across the opening from pharynx to water tube so as to intercept anything passing into the water tube. Nothing further can be seen of this apparatus from the pharyngeal cavity, but if the water tube be opened from the ventral side the velar jaws may be seen in connection with the velar valves

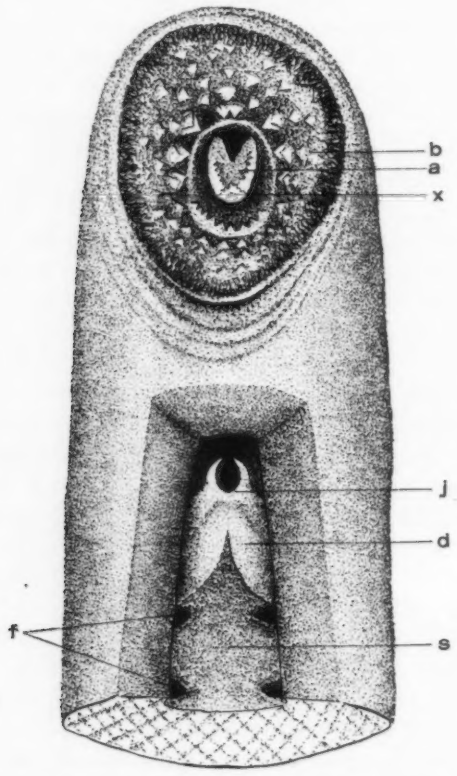

FIG. 6. Ventral view of the head of *P. marinus* with the cavity of the water tube and pharynx exposed. *a*, tongue; *b*, oral funnel; *d*, velar valves; *f*, internal branchipores; *j*, velar jaws; *s*, water tube; *x*, anterior lobe of the tongue.

which guard the passage between the pharynx and water tube (Fig. 6). The velar valves (Fig. 1, *l*, and Fig. 6, *d*) are two semilunar flaps which extend dorso-ventrally, one on either side

of the water tube at its junction with the pharynx. They are united to one another in the middle line for 1 or 2 mm. near their dorsal ends but are free elsewhere, so that there is left between them a slit-like opening. They are concave caudally and their lateral edges are united to the water tube. They function normally to prevent water entering the pharynx from the water tube.

In order to understand the relation between the velar jaws and the velar valves the cartilaginous frame-work common to the two must be carefully dissected out. It is found to bear a striking resemblance to a pair of mechanic's nippers except that it is in one piece, whereas the latter is in two pieces. The jaws of this nipper-shaped cartilage are much smaller than the handles and have a much smaller arc between them. In fact the proportion between the jaws and handles of the cartilaginous apparatus is much the same as is found in the manufactured tool and like it tends to power in grasping. Approximation of the handles of a pair of nippers brings the jaws together. This is due to the fact that the halves of the nippers are crossed and fastened together by a pin. The two halves of the nipper-shaped cartilage are not crossed, hence when the handle is pushed inward, the corresponding jaw moves outward. The jaws of these nipper-like cartilages form the supporting skeleton of the velar jaws found in the pharynx, while the handles extend into the lateral walls of the water tube as slender cartilages which end on its ventral wall just cranial of the first internal gill opening (Fig. 6). The cartilages lie along the lateral attached edges of the velvar valves and support them.

FIG. 7. Cartilaginous skeleton of the velar jaws and valves.

There are three pairs of muscles which are inserted into the nipper-shaped cartilage common to the velar jaws and velar valves. These are the velo-pharyngeus, velo-hyomandibularis internus, and the velo-hyomandibularis externus. They are sufficiently described by Fürbringer (1875), although he does not mention the velar jaws. Their combined action is to move the cartilaginous rods supporting the velar valves (the handles of the nippers) inward and outward. When the rods are moved inward, toward

one another, the velar valves are relaxed and water may pass from the water tube into the pharynx; at the same time the velar jaws are opened. When the rods are separated, the valves are stretched so that they are able to close and the velar jaws are also closed.

C. *Gills.* — In order to get a clear idea of the gills it is necessary to call to mind their supporting skeleton. This consists of nine irregular vertical bars on each side. The first is placed almost immediately posterior to the styloid cartilage, the second immediately in front of the first gill cleft and the remaining seven are one just behind each of the seven gill clefts. These bars lie close to rings of cartilage, which surround the gill clefts but the bars are not continuous with the rings (Fig. 14). The vertical bars are united by four longitudinal bars; one is placed above the gill clefts and one below them, while a third lies along the side of the notochord; the fourth lies close along the mid-ventral line and is connected with the corresponding bar on the opposite side. The cartilaginous pericardial capsule is connected with the ventral longitudinal cartilages at their caudal end and is very elastic. This whole basket lies external to the gill sacs. While it yields to every muscular contraction, yet it is strong enough to lend firm attachment to muscles.

Lying within this frame-work are found the gill sacs. Each gill sac is a somewhat flattened ellipsoid. It is perforated at the ends of its major axis by the external and internal branchial openings. Its shortest axis is caudo-cranial so that we may conveniently distinguish in each sac a caudal and cranial surface or wall, a lateral and medial end, and a dorsal and ventral border. These sacs are not themselves attached to the supporting cartilage, but each lies within a muscular pouch to which it is connected by muscular fibers, and this muscular pouch is in turn attached to the cartilaginous rods of the visceral skeleton on three sides, dorsal, ventral and lateral.

The openings of the gill sacs into the water tube (internal branchiopores) have slightly swollen lips. Those belonging to each pair of sacs are in the same transverse plane. The opening of each pair of gill sacs to the exterior (external branchipores) lie also in the same transverse plane, but in a plane caudal to

that which passes through the internal openings of the same pair of sacs. The principal axis of each gill sac, the axis connecting the branchipores, is thus oblique to the long axis of the body and is directed from its medial end, caudo laterad (Fig. 5, *f*). The gill sac also crosses its muscular pouch obliquely. Its internal opening lies near the cephalic margin of the medial end of the pouch, while its external opening lies near the caudal margin of the lateral end of the pouch. The muscular pouches are larger than the gill sacs, so that the two lie in contact only at their openings, where they are united (Figs. 5 and 8).

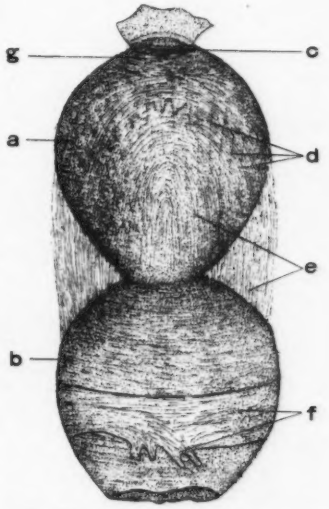

FIG. 8. Gill sac with its muscular pouch. The pouch is cut near its lateral end and reflected from the sac. *a*, gill sac; *b*, gill pouch; *c*, ental muscle; *d*, lines of the gill lamellæ showing through the gill sac; *e*, internal compressor muscle of the gill sac; *f*, deep compressor muscle of the gill pouch; *g*, external compressor of the gill sac.

When the gill sacs are examined from the outside, the lines of attachment of the gill lamellæ are seen (Fig. 8). While the walls of the gill sacs are thus transparent, they are neverthe less covered with a layer of muscle fibers (Fig. 8). These fibers are very delicate and form a thin layer which spreads over the gill sac like a spider's web and might easily escape notice. There are two of these muscles on each side of the sac. They have not hitherto been described. One muscle, *the external compressor of the gill sac* (Fig. 8, *f*), is a narrow band near the external opening of the sac. Its fibers arise from the lateral one fifth of the dorsal and ventral border of the gill sac and form over its surfaces arches with their concavities toward the external opening. The muscle functions in compressing the external one fifth of the gill sac.

The fibers of the larger muscle, the *internal compressor of the*

gill sac (Fig. 8, *c*), arise on the medial one fifth of the dorsal and ventral borders of the muscular pouch. From this origin the fibers spread over the caudal and cranial surfaces of the gill sac not covered by the external compressor. They form arches whose concavities are directed toward the median plane. These muscles function to compress the gill sac while shortening its major axis.

The muscular pouches are placed side by side so that the cranial wall of each and the caudal wall of the next in front of it are in contact. So close do they lie that there appears to be but a single wall separating the contents of the successive pouches from one another (Fig. 5). Most writers indeed speak of the septa between the gill sacs without recognizing their double nature and the resulting muscular pouches. The double nature of these walls can be detected only by the microscope. They are very thin toward the center but become much thicker toward their borders. In preserved specimens a great abundance of coagulated lymph is found between the gill sac and its pouch. The muscular pouches are supported at their external openings by the small rings of cartilage already mentioned as lying close to the last seven vertical bars of the branchial basket (Fig. 14, *b*). These vertical and longitudinal bars of this basket lend support to the pouch on its lateral, dorsal and ventral walls. The medial wall is supported near its center by the wall of the water tube with which it is continuous and by cartilage at its extreme dorsal and ventral ends. These muscular pouches are placed in the cartilaginous basket very obliquely with the medial ends of the major axis craniad of the lateral ends. This added to the obliquity of each gill sac in its pouch causes the gill sacs to overlap each other like shingles on a roof. Nowhere can a cross section be made through the gill region without cutting two gill sacs. A line connecting the internal and external gill openings of any gill sac thus makes an angle of 45° with the long axis of the body.

The fibers of the muscular gill pouch are very difficult to follow on the outside of the pouch on account of the pigment found deposited there, but if the pouches be turned inside out, the fibers may be plainly seen crossing the flattened caudal and

cranial walls (Fig. 8). These fibers form arches convex toward the external opening and end on a narrow raphe on the dorsal and ventral walls of the pouch. The action of these muscles is to compress the whole muscular pouch and to cause its lateral end to be drawn toward the water tube thus greatly shortening its long axis and that of the gill sac.

On the inner surface of the gill pouch, at about the junction of the middle and lateral thirds of its major axis, are found strong bands of muscular fibers, *the deep compressors of the gill pouches*, lying beneath the fibers of the pouch proper. They arch in the same general direction as those already described and end on the dorsal and ventral borders of the pouch as do the muscle fibers of the pouch itself. In the center of the arch, however, some of the fibers run out diagonally toward the external gill opening and are attached to the surface of the gill sac at about the junction of the fourth and lateral fifths of its longer axis. They function in compressing the gill pouch and in fastening the gill sac to the pouch. These bands are found on both sides of the pouch, but are much larger on the cranial side. This may be due to the fact that the gill sac is so placed in its pouch that a greater space is found between the pouch and the sac on the cranial side than on the caudal side. On the caudal side of the internal opening may be seen many blood vessels (branches of the afferent branchial artery entering the gill sac) and these also serve to fasten the sac to the pouch at this point.

If a gill sac be turned inside out, the gill lamellæ may be seen projecting from the inner wall and lying close together like the leaves of a book (Figs. 9 and 11). The lamellæ are found mostly upon the flattened cranial and caudal surfaces of the sac. The lateral or distal end of the sac is but slightly encroached upon by them. The medial end shows a smooth lenticular space around the internal gill opening with its long axis dorso-ventrad. From the edge of this space the lamellæ extend toward the external gill opening. Those at the middle of the caudal and cranial walls of the gill sac (*i. e.*, those lying in a direct line between the gill openings) are the longest. Thence they diminish in length dorsally and ventrally on both sides until those near the dorsal and ventral borders of the gill sac are only about 5

mm. in length. The gill lamellæ do not reach the external opening hence there is left a smooth space about the opening. This space is much wider than the one found about the internal gill opening and extends farther along the dorsal and ventral borders (Figs. 9 and 10).

The lamellæ are attached by one margin along their whole length except near the external gill opening. Here they are broadened abruptly and their ends are free. These enlarged free ends of the lamellæ are somewhat triangular and are bent dorsad or ventrad so that they overlap each other along the edge of

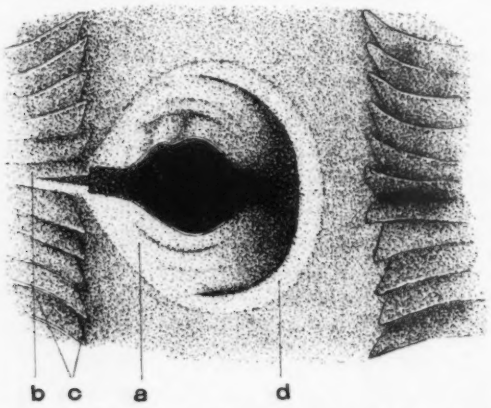

FIG. 9. A portion of the interior of the gill sac showing the external branchiopore with its ental valves in the position they assume when water is entering the gill sac. *a*, ental valve; *b*, central lamellæ which splits and forms the ental valves; *c*, laminæ ending free; *d*, cartilaginous ring of the external branchiopore.

the distal smooth area (Figs. 9 and 11). The central lamella on both the cephalic and caudal walls splits into two laminæ about 10 mm. from its free ends (Figs. 9 and 11, *b*). The laminæ of the cephalic wall end free. When those of the caudal wall reach the edge of the cartilage which surrounds the external gill opening, there extends from each a membranous sheet which forms one of the ental valves (Fig. 9, *a*; Fig. 10, *a*).

Each ental valve is a nearly circular concave plate attached by less than one third of its circumference to the caudal half of the medial end of the external branchiopore. The branchiopore

forms a short tube connecting the gill sac with the exterior. The ental valves extend laterad and at the same time dorsad and ventrad to the outer end of the tubular branchiopore to which the ectal valve is attached. Each has its concave face outward and the two cover about two thirds of the lumen of the branchiopore. Each overlaps its fellow by nearly half its dorso-ventral diameter.

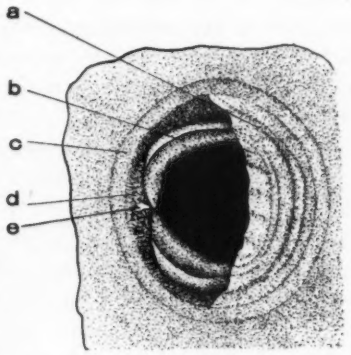

FIG. 10. The external branchiopore showing the normal position of the ectal and ental valves when water is being discharged from the gill sac. *a*, ectal valve; *b*, ental valve; *c*, cartilaginous ring; *d*, buccal fringe; *e*, point on the cartilaginous ring.

The ectal valve is a thin membrane which is attached to the cephalic half of the outer margin of the external branchiopore and stretches loosely over the cephalic half of its lumen (Fig. 9). The ental valve is attached at the internal

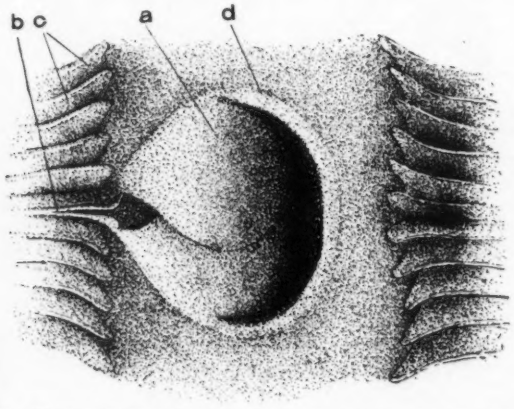

FIG. 11. Position of the ental valves when the ectal valve is stretched taut. *d*, cartilaginous ring; *a*, ental valve; *c*, laminæ of the gill sac; *b*, central divided lamellæ.

end of the external branchiopore and on its caudal margin while

the ectal valve is attached to the external end and on the cephalic margin. When the free border of the ectal valve is tightly stretched in the cartilaginous ring (Fig. 12) the ental valves, if forced outward by pressure within the gill sac, strike against the ectal valve and close the external branchiopore thus preventing the escape of water.

If the border of the ectal valve is relaxed it does not afford a support for the ental valves which are then forced out past it by the pressure of the water and thus permit water to pass out through the external branchiopore (Fig. 10). Thus while the valves of the external branchiopore can at no time prevent the entrance of water into the gill sac, they are able under certain conditions, to prevent its exit.

The stretching of the ectal valve is effected by the action of two muscles which elongate the dorso-ventral axis of the cartilaginous ring to which the valve is attached. The first one is seen when the integument is removed and lies on the cranial side of the gill cleft. This small band of muscles lies loosely around the cephalic side of the gill opening, and is attached to the longitudinal bars immediately dorsal and ventral to the vertical axis of the opening and to the ring of cartilage (Fig. 13). This may

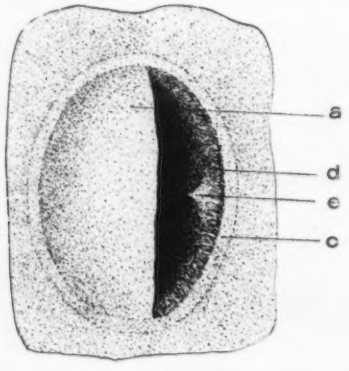

FIG. 12. The cartilaginous ring of the external branchiopore is oval in shape thus stretching the ectal valve taut. *a*, ectal valve; *d*, buccal fringe; *e*, point on the cartilaginous ring; *c*, cartilaginous ring. Figs. 11 and 12, placed back to back as here printed, form together a model of a left external branchiopore with closed valves.

be called the *ectal muscle*.

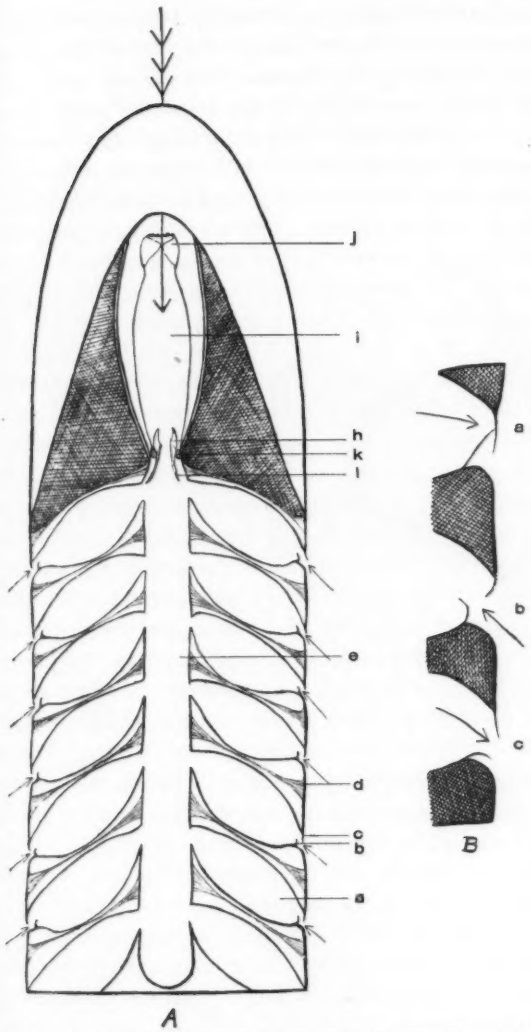

FIG. 13, *A*. A diagram of the respiratory apparatus of *P. marinus*. The possibility of the water entering the gills from the mouth and the external branchiopores at the same time is shown. *a*, gill sac; *b*, ental valve; *c*, ectal valve; *d*, muscular gill-pouch; *e*, water tube; *i*, velar valve; *k*, posterior pharyngeal muscle; *h*, velar jaws; *i*, tongue; *j*, tongue lobe.

FIG. 13, *B*. Diagram of the ectal and ental valves of the external branchiopores of *P. marinus*. *a*, closed valves; *b*, position of valves as water enters the gill; *c*, position of valves when water leaves the gill.

The other half-ring shaped muscle (*ental muscle*) is smaller and extends loosely around the caudal side of the gill sac near its external opening but between the gill sac and its pouch. Thus it cannot be seen unless the muscular pouch be cut and reflected. It is attached to the same longitudinal rods of cartilage as is the ectal muscle, a little beneath the points of attachment of the latter and is attached slightly to the ring of cartilage (Fig. 8, *c*) which sends out a flat semicircular projection. This projection lies on the caudal side of the external gill opening within the ring of cartilage. It bears a slender conical rod of cartilage (Figs. 10 and 12, *e*).

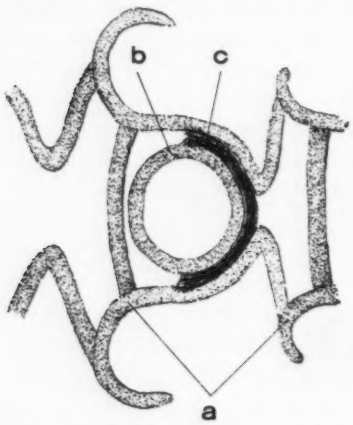

FIG. 14. The ectal muscle and its attachment. *a*, cartilaginous bars; *b*, cartilaginous ring; *c*, ectal muscle.

The ectal and ental muscles are striated and function in compressing the sides of the ring of cartilage so that the naturally circular cartilage becomes elliptical with its long axis dorso ventrad. Cuvier (1840) and Mayer (1835) speak of a circular muscle of the gill opening which lies around the ring of cartilage and serves to close the gill opening. Just how a constrictor muscle, if such a muscle were present, could so compress the cartilaginous ring as to completely close the opening is not clear.

A fringe of hair-like processes lying around the caudal border of the external gill opening deserves mention. Cephalad about 1 mm. from the middle of this fringe is the small cartilaginous projection which is the outgrowth of the cartilaginous ring before mentioned. The function of these outgrowths is not known. They may be tactile.

D. *Nasal Sac.* — The nostril is situated on the dorsal side of the head in the median line about 5 mm. anterior to the paired eyes. This nostril leads into a tube which opens directly into the nasal sac with its olfactory lamellæ. From the cranial por-

tion of the nasal sac there continues ventro-caudad the nasal cœcum which curves around the anterior ends of the brain and notochord (Fig. 1, *f*). This nasal cœcum lies directly under the notochord and ends blindly on a line with the center of the second gill sac. The ventral wall of the tube follows the ethmoid cartilage to its posterior end and is there attached to the pharyngeus muscle as was before noted. It continues caudad from this point. At its caudal end it is parallel to the long axis of the body. The posterior part of the tube which is immediataly above the œsophagus, overlies both its dorsal and lateral walls and rests on the first and second gill sacs for 1 or 2 mm. on each side (Fig. 1).

The result of the position of the tube directly between the anterior end of the notochord and the strong muscles of the gill pouch ventral to it is that it is pressed up against the notochord at every contraction of the underlying muscles. This action of the muscles causes the water in the tube to be forced out of the nostril with considerable force. Upon the relaxation of the muscles to which the tube is attached the sac refills (Fig. 1). Thus, although the nasal tube has no direct communication with the respiratory apparatus, yet the effect is practically as though it had. At every expiration from the gills there is a corresponding expiration from the nostril and with every inspiration water passes into the nostril. The relationship existing between the expired and inspired streams of the nostril and gills has long been known, but hitherto the causes underlying this relationship have not been understood.

(*To be continued.*)

THE EYE OF CRYPTOBRANCHUS.

ALBERT M. REESE.

Since no investigations, apparently, have been made on the anatomy of the eye of the American giant salamander, *C. alleghensis*, a brief description of that organ may be of interest.

In the living animal the eyes are quite inconspicuous, due to their small size, their lack of bright coloration, and to the wrinkled condition of the skin that surrounds them. The pupil, as seen from the surface, is very irregular in outline ; it appears as a small, jagged, black spot in the center of the gray iris. The eyes of the living *Cryptobranchus* do not differ markedly in appearance or relative size from those of *Necturus*.

In order to study their structure, the eyes, with a little of the surrounding tissue, were removed and sectioned in colloidin. Owing to the hardness of the lens it was not possible to cut very thin sections. The tissue was stained *in toto* with borax carmine, and after the sections were arranged serially on the slides they were stained with Lyon's blue. The memorandum as to fixation having been lost, it is not possible to give the method, but the results were fairly satisfactory except in the case of the layer of rods and cones of the retina. The figure represents a section through the middle region of the eye, passing through the optic nerve and the pupil.

The sclerotic coat (*Sc*) is rather indefinite in extent, and is largely chondrified. This cartilage forms a very thick capsule that surrounds considerably more than half of the globe of the eye. It is perforated, of course, at the back for the passage of the optic nerve. The walls of the cartilaginous capsule are not of homogeneous structure throughout, but are penetrated at places by ingrowths of tissue apparently derived from the choroid (*Ig*). The unchondrified portion of the sclerotic is, as has been said, of rather indefinite amount. It extends in front of the eye, between it and the superficial epithelium, to form a comparatively thick and, one would think not very transparent, cornea (*C*). In the fibrous portions of the sclerotic, as in other parts of the

eye, are frequently seen large, black, many-branched pigment cells (*Ps*).

The corneal epithelium (*E*) is a direct continuation of the general epithelium of the head, there being no lids. As seen in the figure, the corneal epithelium is somewhat thinner than that of the rest of the head, and is composed of several layers of small cells with strongly-staining nuclei; the nuclei of the deepest layer are somewhat larger than the more superficial ones.

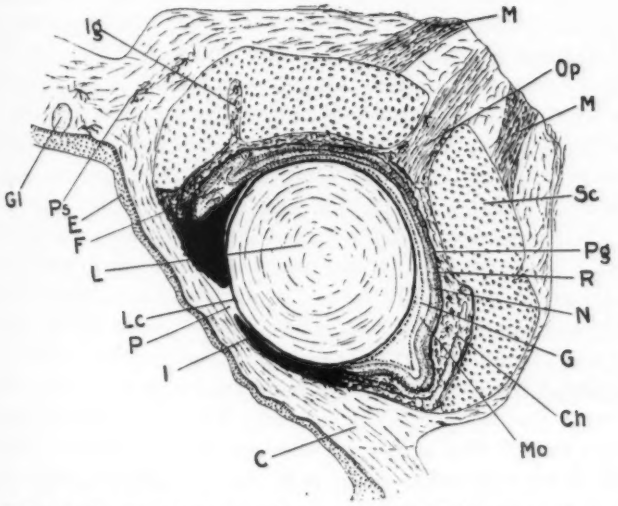

FIG. 1. Section through the eye of *Cryptobranchus Allegheniensis*. *C*, cornea; *Ch*, choroid; *E*, epithelium (conjunctiva); *F*, fold of the retina; G, ganglion-cell layer of retina; *Gl*, gland in the skin near the eye; *I*, iris; *Ig*, ingrowth of choroid into the cartilaginous sclerotic; *L*, lens; *Lc*, lens capsule; *M*, muscles; *Mo*, molecular layer of retina; *N*, inner and outer nuclear layers of retina; *Op*, optic nerve; *P*, pupil; *Pg*, pigmented layer of retina; *Ps*, branched pigment cells; *R*, layer of rods and cones of the retina; *Sc*, cartilaginous sclerotic.

In spite of the fact that the eye seems to have practically no power of motion, there are present the usual muscles, and they are of considerable size; two of them are shown in the figure (*M*).

The choroid (*Ch*) lies in immediate contact with the inner surface of the cartilaginous sclerotic, and is continued in between the front of the lens and the back of the cornea, in the usual

way, to form the iris. It is more or less closely filled with the irregular, black pigment cells that were mentioned in connection with the sclerotic. These cells are seen along the tract of the optic nerve as it passes through the cartilaginous sclerotic. No distinction of layers can be made out in the choroid, nor can a true ciliary process be determined, though a thickening and folding in the region ordinarily occupied by that structure might be interpreted as a ciliary process; no connection of this thickening with the lens can be determined, however, and the appearance of a ciliary process seems to be largely caused by a curious folding of the retina, to be presently described. The reference line *Ch* ends in the thickening just described. In that portion of the choroid that extends in front of the lens to form the iris (*I*) the pigment cells increase to such an extent that the iris is almost or quite black, though this dark color is not so evident in the living eye.

The pupil (*P*) is, as has been said, small and irregular in outline. The retina, though not particularly well fixed in the material studied, shows at least six layers, which may be given the names usually applied to the corresponding structures in other eyes. The outermost (*Pg*) is the pigmented layer; it is comparatively thin, but shows an inner pigmented and an outer nuclear portion. Close to the inner surface of the pigmented layer, though often torn from it, is the layer of rods and cones (*R*); it has been called the layer of rods and cones, though, owing to imperfect fixation, the two structures are indistinguishable. Next to the layer of rods and cones lies a deeply-staining layer (*N*) that, in favorable sections, shows an indistinct division into an outer and an inner zone, which might be called the outer and inner nuclear layers, respectively. The two nuclear layers are composed of similar round, granular elements. Inside of the inner nuclear layer is a finely-granular, nonstaining layer which probably corresponds to the inner molecular layer (*Mo*). The outer molecular layer is not distinguishable in the material at hand. The innermost layer of the retina (*G*), which seems to correspond to the ganglion-cell layer, is composed of a single row of large, rounded or oval elements that stain deeply like the elements of the two nuclear layers. No layer of nerve fibers can

be seen inside of this ganglion-cell layer, nor can the connection of the optic nerve (*Op*) with the retina be determined. The ganglion-cell layer lies, as a rule, in close contact with the lens, so that there is no vitreous cavity; the narrow space that sometimes appears between the inner layer of the retina and the capsule of the lens is probably due to a slight distortion of the eye.

One of the most striking features of this eye is the large surface covered by the retina; it extends as is partially shown on the right side of the figure, for some distance in front of the region of the ciliary process, if the thickening of the choroid may be so called. Another striking feature of the retina is the marked fold seen in the region of the ciliary thickening. All of the retinal layers take part in this fold (*F*), which varies somewhat in complexity in different eyes, but is evidently a normal condition and not a mere artifact.

The lens (*L*) presents no striking peculiarities; it is almost spherical in form, and completely fills the cup of the eye, so that the vitreous cavity, as has been said, is obliterated; a small space between the front of the lens and the cornea (at the end of the reference line *P*) may, perhaps, be taken to represent the aqueous cavity. The lens is surrounded by a comparatively thick capsule (*Lc*), whose distinctness is somewhat exaggerated in the figure.

The correlation of some of the above-described structures with the habits and mode of life of the giant salamander is not difficult to determine, but in other cases the correlation is not so certain.

The flattened anterior surface of the bulb, for example, is seen in most aquatic amphibia and may be merely a measure of protection against injury by coming in contact with the rocks and other objects under which the animal may hide; again a flattened or depressed cornea would evidently offer less friction in swimming.

A cartilaginous sclerotic is common among the amphibia, but it is difficult to see the necessity of such a heavily chondrified sclerotic in an eye that is so deeply buried as is this one. The spherical lens resembles the same structure in the teleosts, and probably indicates that the eye is especially adapted to vision at

short range, the lack of transparency of the surrounding medium making long-range vision impossible, in any case. Although no definite experiments have been made along this line by the writer, it seems probable, from general observations, that *Cryptobranchus* is not very keen of sight even at short range.

The slight development of the ciliary process and the apparent absence of the ciliary muscles make it difficult to see how this animal can have any power of accommodation, since there is nothing that corresponds to the processus falciformis of the teleost eye. It is possible, therefore, that objects are clearly seen only when they are at a certain distance from the eye.

The unusually large extent of the retina may be a compensation for the slight power of motion possessed by the eye as a whole, so that the image of an object may fall upon a sensitive surface even though the object be without the ordinary line of vision.

The absence of the vitreous chamber may be correlated with the unusual refractive power of the lens, which makes a further refractive medium unnecessary, and necessitates the shortening of the eye-ball to bring the retinal surface to the focus of the highly-refractive lens.

SYRACUSE UNIVERSITY,
January 28, 1905.

THE MORPHOLOGY OF THE MADREPORARIA, VI THE FOSSULA IN RUGOSE CORALS.[1]

J. E. DUERDEN.

The term fossula, as employed in the literature of rugose corals, refers to a depression or pit in the calice, due to the smaller size of the septa at that particular region. Generally only one fossula is present in a corallite (Figs. 10 and 11), but there may be three (Figs. 1 and 12), or rarely two or four. The presence of the one or more pits gives a decided bilateral character to the calice, which otherwise might be perfectly radial.

The occurrence of one or more fossulæ has always been regarded as an important characteristic of the extinct Rugosa or Tetracoralla, nothing suggestive of such being found among modern hexameral Madreporaria, and, as would be expected, various explanations have been put forward to account for their presence. The present contribution is an attempt to understand the nature of the fossulæ from the stages passed through in the development of the individual corallite.

Where only a single fossula is present it is situated towards the ventral end of the principal axis of the calice, and where three occur the two additional are lateral and symmetrically disposed; when present the fourth fossula is towards the dorsal extremity of the principal axis. The single ventral fossula is the most persistent and characteristic of the series, and may be known as the main or cardinal fossula, or better, as the ventral-directive fossula, since it is associated with the cardinal or ventral septum. The two lateral are the alar fossulæ, and are dorsal to the alar septa; the fourth is the counter or dorsal-directive fossula.

[1] The first two parts of this series of papers appeared in the *Johns Hopkins University Circulars*, Vol. XXI., Nos. 155 and 157, and were reprinted in the *Annals and Magazine of Natural History*, Ser. 7, Vol. X., May and August, 1902. The third and fourth parts appeared in the *Annals and Magazine of Natural History*, Vol. X., November, 1902, and Vol. XI., February, 1903; the fifth part in the BIOLOGICAL BULLETIN, Vol. VII., July, 1904. The work is being carried out with the assistance of an appropriation from the Carnegie Institution.

Contributions from the Zoölogical Laboratory of the University of Michigan, No. 96.

The Alar or Lateral Fossulæ.

We may first enquire into the nature of the alar or lateral fossulæ, as represented in the calice of a rugose coral such as *Ha-*

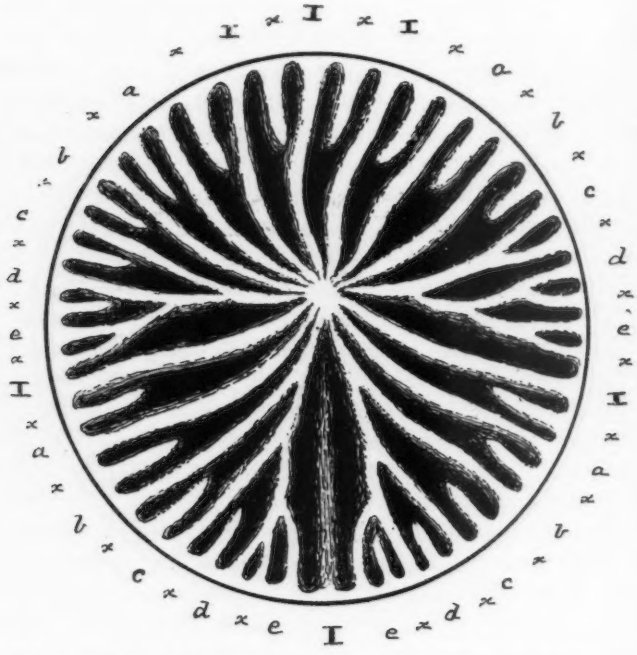

Fig. 1. Calice of *Hadrophyllum pauciradiatum*, E. & H., showing the arrangement of the septa. Here and throughout the figures the Roman numerals I indicate the six primary septa or protosepta, the letters *a–e* the secondary septa or metasepta, and *x* the exosepta making up the outer smaller cycle (see description, Fig. 7); the lower side is regarded as ventral and the upper as dorsal. The two alar fossulæ are formed by the medio-lateral group of shorter septa, *c–e*, on each side, and the cardinal fossula by the ventro-lateral group of shorter septa, *b–e*, on each side, along with the more depressed ventral directive septum (I).

The series, Figs. 2–11, shows the complete septal development of *Streptelasma rectum*, Hall. The drawings were made as the successive stages were exposed on grinding down a corallite; the middle dotted line in each septum represents the line or centers of calcification.

drophyllum pauciradiatum (Fig. 1). The Devonian genus *Hadrophyllum* here chosen is one which Milne-Edwards and Haime,

in their "Coralliaires" (III., p. 334), specially distinguish as having three fossulæ, one axial and two lateral, and may therefore be taken as showing the alar fossulæ in their typical condition. In the figure given each alar fossula is seen to be associated with a few smaller septa (*c*–*e*) which fall short of the center, the shortening varying successively in a gradual manner. Further, each of the shorter septa is inclined dorsally by its inner border towards the next larger septum and is fused with it, so that together they form a group of septa very distinct from the perfect septa, and separated from the alar septum by a somewhat deeper and wider interspace.

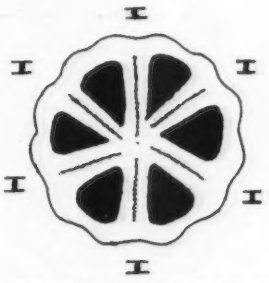

FIG. 2. Primary stage with six equal septa and six interseptal spaces or chambers. The axial septa are the dorsal and ventral directive septa, the former being the *Gegenseptum* and the latter the *Hauptseptum* of German writers; the four lateral septa are the dorso-lateral and ventro-lateral pairs, the latter being the *Seitensepta* or alar septa. The two middle interseptal chambers are the counter quadrants of palæontologists, and the two ventro-lateral are the principal or chief quadrants.

Frequently, however, between the primary alar septum and the group of incomplete septa on its dorsal aspect there is scarcely any special depression or pit present, such as is implied in the term fossula; even individuals of the same species vary much in this respect. Hence it will give a more precise morphological significance to the term if it be extended so far as to refer to the smaller, grouped condition of the septa, whether or not they are separated by a special depression from the alar septum. The subsequent discussion of the alar fossulæ will therefore have reference more to the group of smaller septa in this region than to any actual depression in the calice with which they may or may not be associated. Where the grouping occurs it is always a conspicuous feature of the calice.

The significance of the shorter septa associated with the alar fossula in *Hadrophyllum* can be understood by comparing the series of figures (Figs. 2–11) representing the complete septal development of *Streptelasma rectum*, as revealed by successive sections of a

single corallite.[1] It is seen that each alar or lateral region is that at which new septa (*a–e*) are successively added to the primary six. Furthermore, the additions take place in such a manner that the newer, shorter septa are for some time inclined towards the older, and are fused with them in a unipinnate manner by their inner borders; it is only towards the close of development (Figs 10, 11) that all the septa become free, and are then radially arranged. This inclination and fusion of the newer with the older septa, as well as their smaller size, gives a distinctive character to the alar regions in *Streptelasma* during the various developmental stages, and usually results in a special interval or interseptal space on the dorsal side of each alar septum.

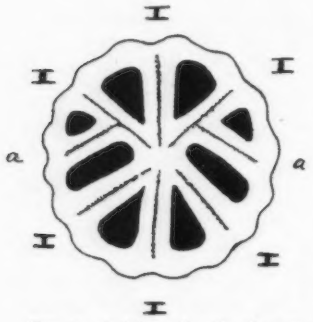

FIG. 3. A bilateral pair of meta-septa (*a*) has appeared, a member within each of the middle chambers or counter quadrants, inclined towards its corresponding dorso-lateral primary septum.

If now the alar regions of Figs. 2–10 be compared with those of Fig. 1, the two alar fossulæ in *Hadrophyllum* are seen to correspond with the two lateral regions of addition of new septa in *Streptelasma*, and both are within the two middle of the six primary interseptal chambers. Hence each alar fossula in the adult corallite of *Hadrophyllum* really corresponds with ontogenetic stages in the establishment of the septa in *Streptelasma*, the septa concerned being those immediately dorsal to the primary alar septum.

That no alar fossula is present at the more mature stages of *Streptelasma* (Figs. 9–11) is due to the fact that as the coral attains its full development the septa become free from one another at their inner border, and at the same time become equal in size

[1] The septal sequence here illustrated is in accordance with Kunth's well known law of septal development found to be characteristic of the Rugosa. Hitherto, it has been generally assumed that only four primary septa are present in tetracorallids whereas six actually occur. However Haeckel's term Tetracoralla has still an appropriateness since the subsequent septa are formed within only four of the six primary interseptal chambers in contrast with the six in Hexacoralla.

and situated at equal distances apart, thereby presenting a more truly radial disposition. On the other hand in the mature corallite of *Hadrophyllum* the septa of the alar region do not reach the radiate condition; they retain their unipinnate arrangement throughout, and, as a consequence, the alar regions remain sharply separated from the rest of the corallite both by a special arrangement of the septa and by an interval.

The series of sections of *Streptelasma* further proves that the alar fossula is situated on the dorsal side of the alar septum; the latter takes no direct part in forming the depression, but merely constitutes its ventral boundary. As shown in Fig. 2, the right and left alar septa are the ventro-lateral pair of the six primary septa, and all the additions in the middle interseptal chambers necessarily take place dorsal to them. In sections the new septa are inclined by their inner border towards the dorso-lateral pair of primary septa, and are thus more nearly parallel with the ventro-lateral (alar) septa.[1] Sometimes, as in *Anisophyllum agas-*

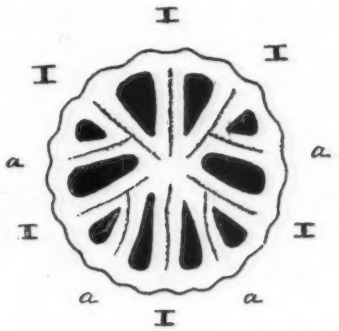

FIG. 4. A stage a little beyond that in Fig. 3. A corresponding pair of septa (*a*) has appeared within the two ventro-lateral chambers or principal quadrants, each member inclined towards a ventro-lateral (alar) primary septum.

[1] In giving the septal plan of a tetracorallid as viewed from above Delage & Hérouard ("Traité de Zoölogie Concrète," II², p. 692, Fig. 973) project the newer septa of the principal quadrants upon the cardinal septum and parallel with the alar septa, while those in each counter quadrant are projected upon the alar septum and are parallel with the dorsal directive or antipodal septum. The figure of *Hadrophyllum* here given, and also those showing the septal development of *Streptelasma rectum*, prove that this is not the true relationship of the inner ends of the metasepta within the calice. In each quadrant the inner end of each septum is from its origin directed towards the next older member of its own series. I have met with no instance in which the later developed septa are inturned towards and fused with the alar and axial directive septa, as seems to be usually assumed from the appearances presented by the external ridges and grooves alone. The explanation which Bourne gives (Lankester's "Treatise on Zoölogy," Art. Anthozoa, p. 73, Fig. 35) of the schematic representation of the septa of a zaphrentoid coral is manifestly self-contradictory as regards the sequence.

sizi, E. & H., the alar septa are much larger than any subsequently developed, and may thus emphasize the fossula adjacent to them. On the other hand, it is very doubtful if the alar septa themselves are ever smaller than the other principal septa, or are situated within the fossular depression, as is sometimes assumed in palæontological works.

Alar fossulæ of a like nature with those in *Hadrophyllum pauciradiatum* have been studied in other tetracorallids, especially in *Microcyclus discus*, Meek & Worthen, *Anisophyllum Agassizi*, E. & H., and also in *Hadrophyllum glans* (White). In these there is the same grouping of successively smaller septa, giving to the alar region its distinctive character. A still larger number of zaphrentoid corals, however, are found to resemble *Streptelasma rectum*:[1] during the earlier stages of development their new septa are related one to another just as they are in the adult of *Hadrophyllum*, while on approaching maturity they become equal and more strictly radial; they all, in fact, pass through a *Hadrophyllum* stage.

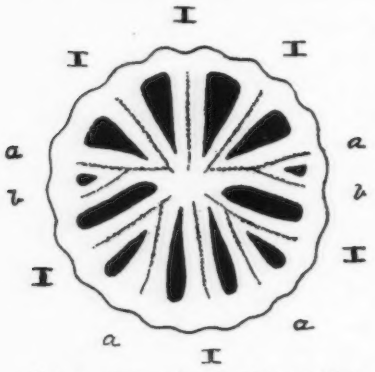

FIG. 5. A second pair of septa (*b*) is now present, one in each of the middle chambers, inclined towards the metasepta (*a*).

The true morphological significance of the difference between adult forms like *Hadrophyllum* with alar fossulæ and others like *S. rectum* in which they are wanting is thus only ontogenetic. In the one development does not proceed sufficiently far as to establish approximate radial symmetry, and the adult corallite

[1] It may be well to state that in the course of the investigations the septal development has been followed by means of serial sections in various species of the following genera comprised within the families Cyathaxonidæ, Palæocyclidæ, and Zaphrentidæ, namely, *Cyathaxonia*, *Duncanella*, *Palæocyclus*, *Hadrophyllum*, *Microcyclus*, *Streptelasma*, *Zaphrentis*, *Lophophyllum*, and *Anisophyllum*. Representatives of the families Cyathophyllidæ and Cystiphyllidæ, particularly the colonial forms, are found to be unsuitable for such studies.

retians the bilaterality of development of its septa; while in the other the bilateral symmetry of growth becomes replaced by a radial disposition of the parts. Whenever alar fossulæ are present they represent an incompletion in the establishment of the newer septa of the alar region, as compared with species in which no alar fossulæ are represented; they have only a developmental significance, and would not correspond with any structural peculiarity of the fully developed polyp. As would naturally be expected from such an explanation even individuals of the same species may vary much with regard to the presence or absence of alar fossulæ. In the calice of some specimens of *Microcyclus discus*, for example, there is a distinct grouping of the alar septa,

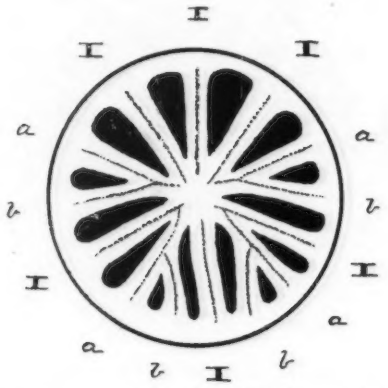

FIG. 6. A corresponding second pair of septa (*b*) has appeared within the ventro-lateral chambers.

while in others the septa have become perfectly radial, and no alar region is distinguishable.

The alar fossulæ represent regions where new septa are being added, and the interspaces may reasonably be expected to be different from the other septal interspaces, and likewise to vary at different stages according as the new septa are just appearing or are nearly fully developed.

From developmental studies the conclusion is thus reached that in all ordinary species of zaphrentoid corals the septa of the alar region pass through a fossular stage as here understood,

whether or not the adult arrangement be radiate; or, stated in another way, the presence of alar fossulæ in an adult corallite is a retention of a developmental characteristic.

The Cardinal or Ventral Fossula.

Enquiry may now be directed into the nature of the cardinal or ventral-directive fossula. This is the most important of the series, being usually represented in mature calices even when all traces of the alar fossulæ have disappeared. Further, its constitution is by no means so simple as that of the alar fossulæ.

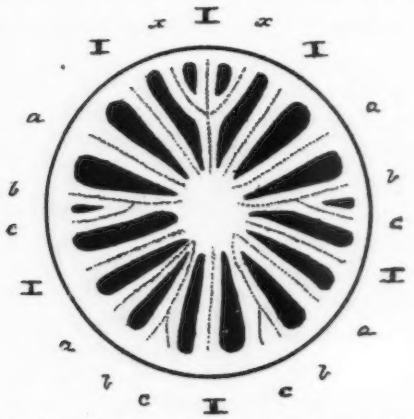

Fig. 7. A third additional metaseptal pair (ϵ) has appeared within both the middle and ventral chambers, the middle pair developing first. A pair of septa (x) has also appeared, one within each of the dorso-lateral primary chambers, fused with the dorsal directive. In relation to the polyp the septa which appear midway between the principal septa are exosepta, and always constitute the outer, smaller cycle in the mature calice; the larger septa, constituting the inner larger cycle, include both the protosepta and metasepta, and are entosepta.

As represented in *Hadrophyllum* (Fig. 1) the cardinal fossula is associated with two groups of successively shorter septa (b–ϵ), a group being situated on each side of the cardinal or ventral directive septum, and, in addition, the cardinal septum (I) is itself smaller than the other fully developed principal septa. The members of each ventro-lateral group of smaller septa (b–ϵ) are related to one another in the same manner as are the members

in an alar fossular group (*c–c*), that is, the shorter septa are turned towards the successively larger, and are united with them by their inner ends in a unipinnate fashion. In general also the space on each side between the group of newly added septa and the axial septum is greater than the other septal interspaces and more pit-like.

Again comparing the adult calice of *Hadrophyllum* with the developmental series of sections of *Streptelasma* in Figs. 2–11,

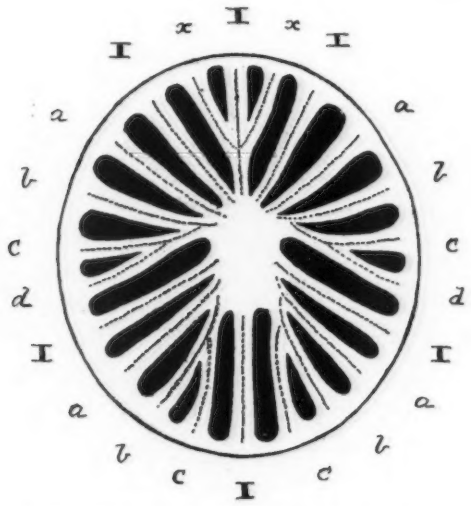

FIG. 8. A stage somewhat in advance of that in Fig. 7. An additional septum (*d*) is present in each middle chamber, while the two pairs, *c*, are much larger. The section shows very clearly the inclination of the septa towards each other in the alar and ventro-lateral regions, only the oldest septa reaching the columella (cf. Figs. 1 and 12).

it is seen that the fossular region on each side of the cardinal septum is a region where the addition of new septa takes place, just as is that on the dorsal aspect of each alar septum. Likewise, the new ventral septa in *Streptelasma* are inclined towards the older and fused with them until the mature condition is reached, when they become free, of the same size as the others, and more nearly radially arranged (Figs. 10, 11). Therefore the cardinal or ventral groups of shortened fused septa in *Hadro-*

phyllum represent a developmental stage when compared with the mature condition of such a form as *Streptelasma;* as in the case of the alar fossulæ, a developmental stage in *Streptelasma* persists as the adult condition in *Hadrophyllum.* The axial cardinal fossula of *Hadrophyllum* is thus shown to be associated with two groups of incompletely developed septa, a group on each side of the cardinal directive septum, while at the same time the latter is much smaller than the other primary septa. Such a

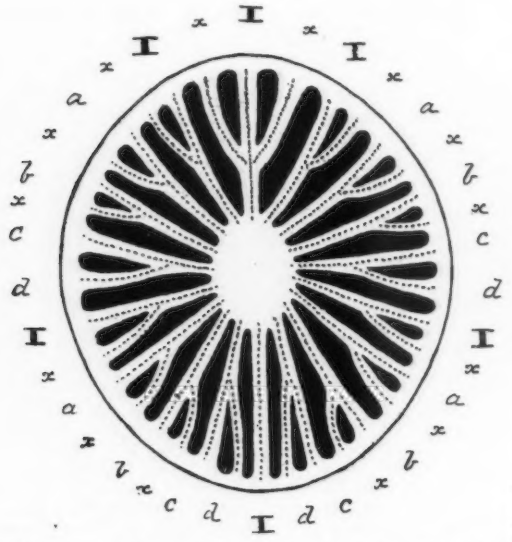

FIG. 9. Exosepta (*x*) have now appeared in association with most of the fully developed septa, namely, all the protosepta (except the ventral directive) and the metaseptal pairs *a* and *b*. The exosepta are at first turned towards and fused with their corresponding dorsal entoseptum.

fossula as a whole may be spoken of as compound, while those in the two alar regions are simple fossulæ.

Studies on other species of rugose corals show that throughout the group the cardinal fossula in the adult calice is constituted either on the *Hadrophyllum* or *Streptelasma* plan; rarely, as in *Anisophyllum*, the cardinal directive septum is much larger than the other primary septa and then the fossula is really double, a

depression on each side of the large axial septum corresponding with the smaller, newly added septa.

As shown in the various figures the cardinal or ventral-directive septum is smaller than the other principal septa, and remains thus when all the other septa have become equal; the axial fossula is then represented in the fully developed calice by the smaller cardinal septum alone, without a special lateral depression on

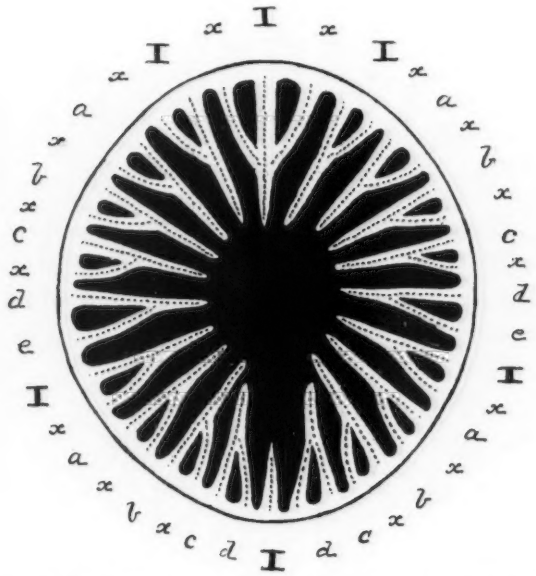

FIG. 10. Section towards the upper part of the corallite. The septa are now free from the columella, and the ventral directive septum is smaller than the others. More exosepta and metasepta have appeared than in Fig. 9, each exoseptum being still fused with its corresponding entoseptum.

each side. Such a condition clearly calls for a different explanation from that given for the alar fossulæ, or for the lateral parts of the cardinal fossula; these have been found to correspond with ontogenetic stages of species which attain nearly perfect radiality in the adult, while the ventral-directive septum in most instances remains shorter even within the mature calice. Manifestly the small directive septum must correspond with some

peculiarity in the polyp itself, an axial peculiarity situated towards the ventral side.

In a paper already published (*Ann. & Mag. Nat. Hist.*, May, 1902), I have given good reasons for supposing that of all modern Anthozoa the living Zoantheæ are most nearly related to the extinct Rugosa. In zoanthids the mesenteries beyond the primary six are added in such a manner as would give the septal sequence characteristic of the Rugosa, that is, the sequence

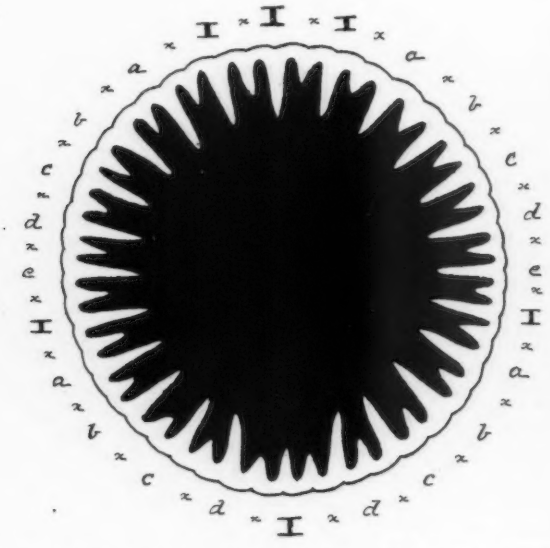

FIG. 11. A section near the upper limit of the corallite. All the septa are now more strictly radial, and those of the inner and outer cycles regularly alternate. There is no distinction in size between the six protosepta (I) and the various metasepta (*a*–*e*), except as regards the ventral directive septum, the smallness of which gives rise to the simple axial fossula.

represented in Figs. 2–10; the only difference is that in modern zoanthids the new mesenteries are added within only the two ventral of the six primary chambers, whereas in the rugose polyps they were added within four of the six primary chambers —the ventral and middle pairs. This difference is, however, but one of detail compared with the actual order of development

of the mesenteries and septa. It is the manner of appearance of the septa beyond the primary six which separates the Rugosa from modern hexameral corals, a separation of the same significance as that by which zoölogists distinguish cyclic hexameral actinians from zoanthid polyps.

The presence of the smaller axial septum in the cardinal

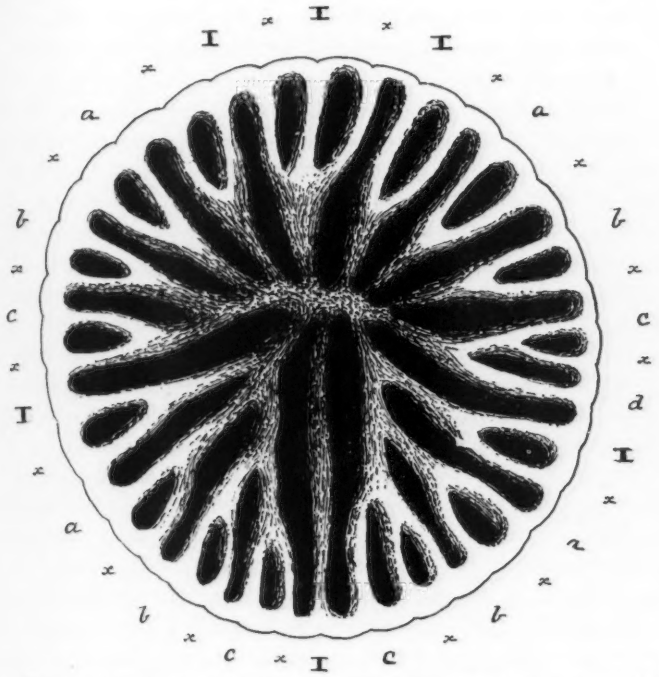

FIG. 12. Arrangement of the septa in a young corallite of *Streptelasma profundum* (Owen). At this early stage the septa are arranged in a manner very similar to those in the mature corallite of *Hadrophyllum* (cf. Fig. 1), while in the fully developed corallite they are nearly radial. The septa show a slight inequality in number on each side, a condition also usually met with in recent zoanthid polyps.

fossula of the Rugosa serves to confirm in a peculiarly direct manner the relationship of the group to the living Zoantheæ. As is well known, one of the characteristics of the zoanthid polyp is the occurrence of a single gonidial groove, sulcus, or siphono-

glyph along the ventral extremity of the stomodæum, as compared with the two opposite grooves (dorsal and ventral) usually present in hexactinian polyps. The single groove in zoanthids is usually well-developed, and its walls often project for some little distance within the ventral directive entocœlic chamber, and are frequently continued into the polypal cavity beyond the rest of the stomodæal wall. It is strongly ciliated and is concerned chiefly in the circulation phenomena of the polyp, sometimes remaining open when the mouth is otherwise closed by the approximation of the lips.

The occurrence of the single gonidial groove gives a marked contrast to the two extremities of the stomodæum of zoanthid polyps, and a decided bilateral character to transverse sections. Manifestly it is the presence of just such a structure which we should expect to result in a diminution of the axial septum were a skeleton formed beneath it; indeed, with such a stomodæum, having a groove at one end and not at the other, we could scarcely expect that the two extremities of a corallite would be alike. In the absence of the rugose polyp itself, no surer proof of the relationship of the group to the zoanthids could to my mind be adduced than that which admits of the correlation of the simple cardinal fossula with a ventral stomodæal groove.[1]

On the above explanation it may reasonably be asked why no corresponding axial fossulæ are found in the calices of recent corals. In answer to this it can be affirmed that as yet we have no certain instance of the presence of a gonidial groove in the stomodæum of modern coral polyps. In the polyps of over thirty species of West Indian corals which I have examined there was no evidence of such a groove, and the same can also be said of a like number of Pacific corals. The stomodæum of coral polyps is comparatively short, and presents the same histological structure all round, showing there is very little if any physiologi-

[1] Other evidences of bilaterality and axial differentiation are sometimes presented by zoanthid polyps. In living examples of *Zoanthus* the axial tentacle over the ventral directive entocœle is frequently larger than any of the others; sometimes the coloration along the dorso-ventral axis is different from that elsewhere; and I have also found the disc to be actually grooved or depressed along the axis. The Ceriantheæ are also characterized by the possession of a single siphonoglyph, but the manner of addition of the mesenteries in this group precludes any relationship with the Rugosa.

cal differentiation associated with its extremities. In this respect living coral polyps differ from the closely allied skeletonless hexactinians, where a gonidial groove usually occurs at each extremity of the stomodæum.

An examination of other species of rugose corals demonstrates that the cardinal fossula is somewhat similarly constituted throughout the group. The two extremes of its development are the complex condition met with in forms like *Hadrophyllum* and the simple modification present in the mature calice of *Streptelasma*. In the one we have it associated with a grouping of incompletely developed septa on each side of a feebly developed axial septum, while in the other it is represented by the smaller axial septum alone. The fossula in the first has an ontogenetic as well as a morphological significance, while in the second it is correlated with a structural peculiarity of the mature polyp. In zaphrentoid corallites in which the calcareous material has been replaced by silica, and the septa are exposed throughout their vertical length,[1] the entire series of developmental changes undergone by both the alar and the cardinal fossulæ can sometimes be observed at a glance, confirming the results obtained from a series of sections like that shown in Figs. 2–11.

The condition in rugose corals with the newly added septa arranged bilaterally in four groups, distinct from the other septa, I propose to term the *Hadrophyllum-stage*, since it is so characteristically displayed in this genus. In general it will be associated with three fossulæ. In its significance the stage is comparable with that of the *Edwardsia* or *Halcampa*-stage met with in some mature actinians and the polyps of modern corals, and passed through in the ontogeny of others. All the simple Rugosa, namely those embraced within the group Zaphrentoidea, exhibit the *Hadrophyllum*-stage for a longer or shorter period during their development; in some it is retained at maturity, while in others it is replaced by a more nearly radial condition of the septa.

[1] For beautifully perfect silicified specimens of *Streptelasma profundum* (Owen), with all the interseptal matter removed by decalcification, I am indebted to Prof. F. W. Sardison, and for others from the geological collections of the University of Michigan to Prof. I. C. Russell. For many other species of Rugosa from the National Museum I am under obligations to Prof. C. Schuchert, and from the British Museum to Dr. F. A. Bather.

The ontogeny of the various forms shows that the shorter septa associated with the fossulæ cannot be considered as representing a cycle or cycles different from the others. Polycycleism, as we know it in the hexacorallids, does not occur in the tetracorallids; however many septa may be developed there are only two cycles represented, the inner larger septa being entosepta while the outer shorter are exosepta. The entosepta include the six primary protosepta and the later metasepta, some members of the former being at times larger than the rest (*Anisophyllum*). In *Menophyllum* the metasepta formed within the middle and ventral chambers differ greatly in size, those in the two ventral chambers being the larger. In this genus three fossulæ are said to occur, the two lateral situated as before on the dorsal aspect of the alar septa; the alar septa are not, as is generally assumed, included within the fossula itself.

As stated in the introduction, a fourth or dorsal-directive fossula is sometimes present in rugose corals, but this occurs very rarely, *Omphyma* being given as an example. Among a collection of *Zaphrentis compressa*, E. & H., from Spergen Hill, Indiana, I have found several in which there is in the mature corallite a conspicuous fossula towards both the dorsal and ventral extremities of the principal axis, the ventral fossula being the more pronounced. In the majority of specimens, however, there is no hint of the dorsal pit. The dorsal fossula would appear to have no developmental significance, since the septal arrangement is there the same as in other species of this genus; rather, it would seem to correspond with some peculiarity of the adult stomodæum, perhaps with the longer continuation of its dorsal extremity.

Radial and Bilateral Symmetry.

A comparison of rugose corals having bilateral symmetry with those in which all the septa are radially arranged introduces considerations with regard to symmetry in corals generally. Mature corals and actinians, like most cœlenterates, are characterized by a more or less perfectly radial symmetry as regards their mesenteries, tentacles, and septa, yet throughout the course of their development these organs follow a decided bilateral method, both in the earlier and later stages.

So far as concerns modern corals I have lately shown (BIOL. BULL., July, 1904) that the septa, correlatively with the mesenteries, present very marked bilateral phases during nearly the whole of their ontogeny; it is only as the organs attain maturity that they become radially symmetrical.

Likewise the study of the development of a large number of rugose corals by the method of grinding proves that they are all characterized by a bilaterality of growth after the protoseptal stage; in the majority of species the bilaterality passes into a radial stage, but in some it is retained at maturity. The bilaterality of the Rugosa is however of an altogether different nature from that of modern Madreporaria; the septa in rugose corals are added as bilateral pairs at only four regions of growth, two on either side, whereas in modern corals the additions are made all round the periphery within the six primary interseptal spaces. Notwithstanding these developmental differences a more or less radial symmetry is reached by the adults of both groups. Little or no importance is thus to be attached to the old distinction that the Rugosa are bilaterally symmetrical while recent corals are radial; the species of both are ontogenetically bilateral, and the degree of radiality attained by the adult varies much in forms otherwise closely related, or even in individuals of the same species. Developmental bilaterality and mature radiality are just as much a feature of the extinct Tetracoralla as they are of recent Hexacoralla.

The more or less perfect radiality of the different groups of the cœlenterates as a whole is reached from very different developmental conditions, as can easily be seen from a survey of what is known with regard to the early stages of the organs in the scyphomedusæ, actinians, zoanthids, cerianthids, and recent and fossil corals. It follows that the adult radiality of organs which arise in such widely divergent manners in no way implies morphological relationship among the animals possessing them. Rather, it is an adaptation to the uniformity of environmental influences on all sides to which sessile or floating organisms are subject. The manner in which the organs arise seems immaterial; however varied the origin the same end is attained at maturity. The feature in the Rugosa here sought to emphasize

is that while the majority pass through their bilateral developmental stages and attain practical radiality, some retain the early bilaterality, evidenced by the presence of one or more fossulæ, The single stomodæal groove of the polyp, correlated with an axial fossula in the skeleton, is the only deep-seated character uninfluenced by the equality of the environmental influences, and usually precludes the attainment of perfect radiality among the Rugosa.

Why should certain rugose corals when mature retain the developmental bilaterality of the *Hadrophyllum*-stage while others continue their growth until their septa attain the radial condition? The former has been shown to be an early ontogenetic stage of all forms, hence rugose corals with alar fossulæ and a compound cardinal fossula are at a lower developmental stage than those attaining radiality. How far the differences are chronological seems uncertain, for some of the earlier Rugosa are as nearly radial as their later representatives, and the adult *Hadrophyllum*-stage was apparently no more common in earlier than in later Palæozoic times. According to Zittel ("Text-book of Palæontology," *Eng. Ed.*, p. 74), the distribution of certain genera characterized by a well-marked *Hadrophyllum*-stage is as follows: *Baryphyllum*, Devonian; *Hadrophyllum*, Devonian; *Anisophyllum*, Ordovician to Devonian; *Menophyllum*, Carboniferous Limestone; *Microcyclus*, Devonian. Others having a more nearly radial disposition of the septa in the adult are distributed in time as follows: *Streptelasma*, Ordovician to Carboniferous; *Zaphrentis*, Silurian to Carboniferous; *Cyathaxonia*, Carboniferous Limestone; *Duncanella*, Silurian; *Palæocyclus*, Silurian. Obviously both forms of corallite, bilateral and radial, were living together during the greater part of the Palæozoic age.

When the majority of trifossulate zaphrentoids are compared with the radial forms, the former are seen to be short, flat, or trochoid corallites, the latter long and conical; also the trifossulate species are usually smaller and have a fewer number of septa. It would seem that corallites with considerable vertical height have had the opportunity, as it were, to outgrow their developmental bilaterality, and their septa have assumed the radiality of maturity, while this has not been the case with the short flat

forms; wherever continuous vertical growth takes place, without the addition of new septa, radiality tends to be assumed by the septa already formed. In elongated forms a considerable vertical interval occurs between the insertion of each new bilateral pair of septa and an approximate radiality is attained, to be again destroyed on the addition of another pair. Somewhat similar changes have been shown to be also characteristic of the growth of modern hexameral corals; the developmental stages are bilateral, but between one stage and another an approximate radiality is reached. As regards the Rugosa it may be accepted as a general rule that developmental bilaterality at maturity is associated with shortness of calicular form.

It does not appear from systematic works that the presence or absence of fossulæ has proved to be a character of much taxonomic value. It is conceivable that forms otherwise closely allied may vary as to whether or not the septa at maturity attain the radial arrangement. The facts already adduced prove, however, that in any series of closely allied forms those with well marked fossulæ represent an earlier phylogenetic stage than those attaining radiality, but beyond this it does not yet seem possible to go.

Explanation of the Fossula.

Concerning the significance of the fossulæ the view here maintained is that they are due to two distinct structural features: (1) a grouping of smaller incompletely developed septa at the region of growth within the middle and ventro-lateral pairs of the six primary interseptal chambers (counter and principal quadrants); (2) in the case of the cardinal fossula only, a smaller ventral directive septum correlated with the presence of a single stomodæal groove in the polyp. The alar fossulæ are altogether the result of the first condition, while the cardinal fossula is either dependent upon a combination of both the first and second causes, or is entirely due to the second. Exceptionally, as in *Anisophyllum*, the cardinal fossula is due only to the first, when it appears as a double depression.

Other explanations of the origin of the rugose fossulæ have been offered. The view hitherto generally accepted is that which regards them as a sort of chamber for the hypertrophied mesen-

teries bearing the sexual products of the polyp. This was first suggested by Moseley (*Q. J. M. S.*, XXII., p. 394), from his studies of the living coral *Seriatopora*, in the following words: "The presence of the deep pits in *Seriatopora* for the reception of the single pair of generative mesenteries and their hypertrophied mesenteries may possibly explain the pits occurring amongst the septa of some palæozoic corals which may have had a similar function."

This theory has met with general acceptance only among English writers, particularly Nicholson, Ogilvie, and Bernard. It is founded entirely upon conditions met with in the modern *Seriatopora*. In the polyps of this genus, only the six primary pairs of mesenteries are present, the first developmental pair being by far the largest and bearing the gonads. In other corals, *e. g.*, *Pocillopora*, *Porites*, and *Acropora* (*Madrepora*), a like inequality, though to a less degree, is met with wherever only the six primary mesenteries occur, but as further cycles of mesenteries appear the six primary pairs become equal and are all fertile; moreover, in zoantharian larvæ the first pair of mesenteries often greatly exceed the others in the extent of their development. As regards their mesenteries the adult polyps of *Seriatopora* are merely at an early phylogenetic stage, and the skeletal pits are correlated with this. Our knowledge of the Anthozoa as a whole gives no support whatever for thinking that any of the mature rugose polyps had only two or even only a few reproductive mesenteries. Rather, the large number of principal or first cycle septa occurring in rugose corals, all more or less equal, gives good reason for assuming that a correspondingly large number of mesenteries would be fertile, as in the polyps of recent Zoantheæ, and also that such fertile mesenteries would be distributed all round the polyp. Moreover, Moseley's suggestion would explain only the occurrence of the pair of deep pits, one on each side of the primary septum; it would not account for the smallness of the axial septum itself.

Bernard[1] (1904, p. 10), while accepting that the use assigned

[1] Bernard, H. M., "The Prototheca of the Madreporaria, with Special Reference to the Genera Calostylis, Linds., and Moseleya, Quelch," *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XIII., Jan., 1904.

the fossula, as a sort of crypt for the sexual products, is probable enough, considers that this need not have been the cause of its origin. Rather, he would explain its presence on the mechanical assumption that at an early stage in its development the coral falls over, and in recovering the upright position the soft polypal parts detach themselves from the base of the prototheca in such a way as to bag down, and thus produce a pit or depression on the floor of the calice. Bernard thus expresses it: "The fossula has a very simple explanation, if the assumption of the falling over is correct. As the soft parts detach themselves from the base of the prototheca they might be expected to bag down, and they will continue to be acted upon by gravitation and drawn over towards the convex side of the coral until the vertical position has been regained. It is possible that this bearing over to the side may be due to the efforts of the polyp itself to bend up, but gravitation in a *causa efficiens*."

Such a purely mechanical explanation is very unsatisfactory when we consider how hypothetical is the conception of any general falling over of the prototheca, and also of the influence which this would have upon the polyp itself as well as upon the corallite; it is difficult to conceive of the bagging down of the polypal tissues always at a definite region of the calice on each side of the cardinal septum. The view which I have submitted above, that the simple cardinal fossula is correlated with the presence in the living polyp of a gonidial groove or siphonoglyph, is more in harmony with the facts of anthozoan morphology, while there can be no question as to the significance of the grouping.

Bernard fails to see the evidence for the existence of more than one true fossula in any coral examined by him. He finds this usually on the convex or "dorsal" side, this being the side which I have here termed ventral, as being more in agreement with the accepted anthozoan terminology. The occasional presence of the fossula on the concave side he attempts to explain as dependent upon a shallower more open prototheca than that in which it forms on the convex side.

Some of Bernard's other statements seem so contrary to all that we know of the nature and development of the Rugosa that

I refer to them here, although not directly bearing upon the fossula. He makes the supposition (p. 11) that "The falling over of the prototheca will explain the departure from a strictly radial symmetry of the septa seen in these curved Palaeozoic corals." He also remarks: "Further, it has long been known that, as such corals gradually reacquire a vertical position, the septal arrangement slowly gives up the bilateral and returns to the radial symmetry. Thus the character on which it was proposed to found a great division of the stony corals was nothing but a slight mechanical adaptation to a passing phase in the life of each individual coral. But it is only fair to say that the whole tendency of recent works on corals has been to discover the invalidity of the supposed division Tetracorallia."

In a previous section (p. 42) I have dwelt upon the significance of bilateral and radial symmetry in corals, and have shown that in both modern and fossil corals the developmental stages throughout are bilateral, and that it is only towards maturity that the most nearly perfect radiality is assumed. It is the order in which the mesenteries and septa appear in corals which gives their distinctive significance to modern and extinct forms, not their bilateral or radial symmetry. Even the first six pairs of mesenteries which arise before any skeleton appears are arranged in a strictly bilateral manner in modern corals, and the subsequent mesenteries and septa also follow the bilateral plan. When fully developed the majority of rugose corals are as perfectly radial as are modern corals. The statement "that the whole tendency of recent work on corals has been to discover the invalidity of the supposed division Tetracorallia" is made on only a partial view of the case. The only recent discovery of any importance in support of Bernard's position is the demonstration, mainly by Miss Ogilvie, of the unity of microscopic structure of the skeleton of rugose and modern corals, a discovery which was to be expected considering that the polyps forming the two groups of skeletons belong to one group, the Zoantharia. Even the discovery by the "Challenger" of the coral *Moseleya*, which, from Quelch's account, was hailed as a living representative of the Tetracoralla, and as breaking down their distinction from living corals, is shown in Bernard's present paper (p. 24) to be alto-

gether unworthy of the importance attached to it, though on grounds which I do not consider the most fundamental. My demonstration that the protoseptal stage of rugose corals is hexameral, like the corresponding stage in modern corals, proves that the Tetracoralla and Hexacoralla are more closely related than has been supposed, even though from this stage they diverge to the same degree as do modern zoanthids and hexactinians. Bernard's assertion is in harmony with others published by Bourne and Ogilvie. In making such these authors have wholly neglected or minimized the significance of the difference in septal sequence between fossil and modern corals, and hitherto it is only such a character which has rendered possible a natural classification of the Anthozoa. Morphologists and systematists know of no character among the Anthozoa of greater value for taxonomic purposes than the mesenterial (and septal) plan. The hexameral protoseptal stage indicates that the tetracorallids and hexacorallids have a common ancestry, but beyond this stage we have no evidence as to their relationships; we have no forms which indicate how the divergence took place, any more than we have for the soft-bodied hexactinians and zoanthids. We cannot think of them as one group derived from the other, but as divergences from a common ancestry.

When this account was practically completed I received three papers from Prof. N. Yakovleff, all devoted to studies of the Rugosa.[1] One, "Ueber die Morphologie und Morphogenie der Rugosa," contains special reference to the subject of the present contribution, and calls for notice. Yakovleff has found that in Russian specimens of *Lophophyllum proliferum* the concave and convex sides of the corallite are the reverse of those in American specimens. In Russian examples the main or ventral-directive septum occurs on the convex side, while in the American it is on the concave side of the coral, the ventral axial fossula varying in

[1] 1. "Die Fauna der oberen Abtheilung der palæozoischen Ablagerungen im Donez-Bassin. II., Die Korallen," Mém. du Comité Géologique, Nouv. Série, Livr. 12, 1903.

2. "A Contribution to the Characteristic of Corals of the Group Rugosa." *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XIII., Feb., 1904.

3. "Ueber die Morphologie und Morphogenie der Rugosa," Ver. der Russisch-Kaiserlichen Mineralogischen Gesellschaft zu St. Petersburg, Bd. XLI., Lief. 2, 1904.

like manner. Although in the great majority of rugose corals the ventral-directive septum (Hauptseptum), along with its associated fossula, occurs on the convex border, yet Yakovleff finds the relationship to be occasionally reversed. Such differences the author considers to be a mechanical necessity in the formation of the secondary septa, according as to whether the mouth or oral surface of the living polyp was inclined to one side or the other of the corallite. In the majority of cases it is supposed that the oral disc was inclined towards the concave side, whereas when the ventral directive septum is on the concave side, the polypal disc was directed towards the convex border.

From Yakovleff's account it is evident that various authors have been misled as regards the orientation of the corallite by assuming that the concave and convex borders are morphologically the same throughout. As he points out, the only reliable criteria for purposes of orientation are the relationships of the septa among themselves. Though the axial fossula may occur on either the convex or the concave side of the corallite, it is always associated with the cardinal or ventral-directive septum; the ventral border may be either convex or concave, or indeed at any angle to the concavo-convex axis, according to the species or even individual.

Yakovleff investigates rather fully the claim which has been made for the occurrence of three or four fossulæ in certain species. With regard to *Omphyma* he shows that the presence of more than one depression is doubtful, as also in the genus *Menophyllum*. He concludes for the Rugosa in general that only one fossula, the ventral-directive, is really determinable, the others resting upon insufficient evidence. In support of this he refers to Bernard's statement, already quoted, that he fails to see the evidences for the existence of more that one true fossula in any coral.

In connection with this I would say that whether the alar region with its group of smaller septa, and more or less special interspace, be included within the term fossula is merely a matter of definition. In the forms already referred to (p. 44) such special regions among the septa do occur, and correspond with developmental stages of others in which they are absent at

maturity. They have been described as fossulæ by all writers hitherto, and the purpose of the present paper is to show the true morphological significance both of them and of the axial fossula. It must be admitted, however, that the axial fossula is the only one corresponding with any structural peculiarity (siphonoglyph) of the mature polyp.

It is also incorrect to say that a fossula never occurs on the dorsal border of the corallite in association with the dorsal-directive septum. As mentioned on p. 42, specimens of *Zaphrentis compressa* occasionally show a marked depression in this region, of the same nature as that on the ventral border.

As would be expected, Yakovleff (p. 408) is unable to accept Bernard's explanation of the fossula as due to a bagging down of the basal tissues consequent on the overturning of the prototheca. He also (p. 400) shows the untenable nature of Bernard's view that the bilaterally symmetrical Rugosa have risen from the radially symmetrical Madreporaria as a result of the falling over of the corallite.

Yakovleff (p. 402) evidently shares the general view that the fossulæ are due to the presence of smaller *primary* septa; "Die Septalgruben sind Viertiefungen, die sich bei den primären Septen befinden . . . in den Septalgruben zeichnen sich die primären Septen gewöhnlich durch ihre schwache Entwickelung (geringen Dimensionen) aus." I have shown above (p. 32) that though the alar fossulæ are always associated with a group of new smaller metasepta yet the primary alar septa (protosepta) are not smaller than the other primary septa; they form the ventral limit of the alar fossulæ, but themselves take no part in any depression or enlarged interspace. Only the ventral axial fossula has associated with it a smaller primary septum, and this constitutes its fundamental distinction from the lateral depressions.

Summary.

1. The two alar fossulæ present in certain rugose corals correspond with the region of addition of new septa within the middle two of the six primary interseptal spaces, and each is situated on the dorsal aspect of a ventro-lateral or alar septum. The fossula is due to the fact that some of the septa are here shorter,

and are inclined towards and fused in a successive manner with the dorsal older septa.

2. Alar fossulæ indicate with an incomplete stage in the radial development of septa, and similar stages are passed through in the ontogeny of other rugose corals in which the mature calice attains more nearly radial symmetry.

3. The cardinal or ventral-directive fossula where best developed is formed by two distinct structural elements: (*a*) a group of incompletely developed septa on each side of the ventral directive or cardinal septum, and (*b*) a ventral directive or cardinal septum smaller than the other septa of the first cycle.

4. The two ventral groups of incompletely developed septa have a significance similar to that of the alar fossulæ, that is, they represent a developmental stage.

5. The smaller cardinal septum was probably correlated with the presence in the rugose polyp of a ventral siphonoglyph or gonidial groove in the stomodæum, like that which occurs in the living Zoantheæ.

6. In the most radially developed species the simple cardinal fossula is represented by only the shortened directive septum.

7. Like modern corals and cœlenterates generally all the Rugosa exhibit bilateral symmetry during their development, and as they approach maturity they become more or less radial.

8. The bilaterality and radiality of tetracorallids and hexacorallids are of very different origin and character, and along with other characteristics of the two groups do not imply any relationship beyond the protoseptal stage.

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THE POSTGLACIAL DISPERSAL OF THE NORTH AMERICAN BIOTA.[1]

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1. INTRODUCTION.

During the last few decades there has been a remarkable accumulation of data on the geographical distribution of the extra-tropical North American biota. In addition to the facts themselves there has been a great advance in those allied sciences which throw some of the most important side lights upon distributional problems—the physiographic and geographic histories of definite areas.

It is of interest to know that the leading factors in this increase in our data have been the surveys by our National Government, especially the work of the U. S. Biological Survey, State Surveys and the great activity of our larger museums, although specialists and amateurs must not be overlooked.

While among many groups there have been notable advances, yet for others our knowledge remains very incomplete, and must apparently remain so because of the immensity of the field and the scarcity of workers. Here even the preliminary organization of data is yet to be made. The recent advance then in distribu-

[1] Read at the Eighth International Geographic Congress, Washington, September 9, 1904.

tional work has been largely due to the great increase in the amount of data.

The next general step of advance which we may expect to follow this stage of rapid accumulation of facts is that of their explanation or interpretation. At present this phase of the subject is much confused by the babel of opinions as to the relative importance of various influences controlling distribution. There are several points of view, and each worker is keen to the influence of certain factors. It is to be hoped that this diversity of opinion will lead to a period of discussion, enriched by many suggestions and discoveries of relations, previously unnoticed. Such a period would certainly hasten the correlation and interpretation of much miscellaneous and imperfectly organized data.

It is to one phase of the subject of faunal interpretation, and the dynamic aspect of the historic factor in particular, to which special attention is directed in this paper. That the historic factor is a real one is very generally recognized, and yet in spite of this fact it is difficult to fully realize that the present distribution which we see, is largely an *effect* of past conditions; the cumulative result of many factors, and not controlled altogether by the conditions of the present environment. To properly estimate this factor it becomes necessary to reconstruct the successional relation and the past conditions, and thus see how each stage has prepared the way for the following one. We must reconstruct the past, for this is as essential in geographical distribution as is the restoration, in the mind of the paleontologist, of the soft parts of the fossils he wishes to interpret.

Some phases of this subject are much more simple than others, just as the history of one region may be much simpler than another. From the biological standpoint this is certainly the case with that part of North America repopulated during the decline of the Wisconsin ice sheet.

To fully understand the return movement to the glaciated region, it is necessary to know the time relations of the various Pleistocene deposits of fossils, as during that time there flourished a variety of forms no longer members of our present fauna. The mastodon, mammoth, peccary, camels, tapirs, native horses and many other forms were then abundant. But, as this phase of

the subject is unfortunately in a very chaotic state little help can come from this source at present. Yet there are certain facts derived from these fossils which are very significant. For example, the occurrence in Pleistocene times (Hay, '02; Hatcher, '02) of such arctic types as the walrus in Virginia and South Carolina along the Atlantic coast, the musk ox in Pennsylvania, West Virginia, Kentucky, Indian Territory and Iowa, and the reindeer in New Jersey, Pennsylvania, Kentucky and Iowa, certainly shows that an arctic climate once reached far to the south. Although limited, this information clearly suggests the general extreme southern limit reached by the arctic types during the Ice Age. As the Wisconsin Ice Sheet was not the maximum one in southern extension, these arctic types, in their last migration in all probability, did not start from this extreme southern limit, but to the north of it. This gives us an approximate starting point in eastern North America of the Postglacial return of life to the glaciated region. From the Great Plains westward the ice sheet did not extend far to the south in the United States so that the return movement in that region began much farther to the north, near the Canadian boundary. At present, as has been said, paleontological facts do not greatly aid in understanding the early Postglacial northward extension of the biota. But there is another source of information to which we may appeal and that is to the affinities or relationships of the biota south of the ice margin. This makes it necessary to take into account the general conditions of life in North America south of the Wisconsin ice margin, and hence to the areas of preservation which must have existed in North America during the Ice Age.

2. Biotic Preserves During the Ice Age.

Repeated glaciation had almost sterilized the northern part of the continent. From whence then came the life now occupying that region? Many of the problems involved in a reply to this question cannot be answered at present, but others may be, in an approximate manner. Much exploration remains to be done in northern Asia before we can hope to answer certain questions on those elements in our fauna and flora which have decided Asiatic affinities. But when we consider the more characteristic

American elements, a much greater degree of definiteness may be secured. From our knowledge of the distribution and conditions of life of the present biota, it seems that while the northern part of the continent lay deeply buried under the mantle of the Wisconsin ice sheet there existed, in all probability, south of the ice margin three distinct belts of life (Adams, '02, *b*). At or near the ice margin, and perhaps only forming a narrow transcontinental belt, was the tundral or barren ground biota. Below this first came stunted trees and shrubs, and farther back coniferous forests forming a transcontinental belt, but composed of two distinct types, an eastern and a western one. Below this, in turn, came a third belt of still less homogeneity; in the east it was composed of deciduous forests and their associated fauna, while in the west it was made up of plains and desert types of life.

With these conditions in mind let us now turn to a more detailed consideration of the various elements which go to make up these belts of life, and attempt to follow some of the dynamic phases which this biota has shown since Glacial times. The fundamental idea in following these dynamic changes is that we have belts of physical conditions migrating to the north. Thus there has been given a definite trend to the environment. This fact cannot receive too much emphasis. Just as when studying the littoral fauna of a pond or lake it becomes necessary to bear in mind the dynamic tendency of this littoral zone — that is for it to move inward toward the deeper water — so in a similar manner, to understand the dynamic changes in life areas or zones we must bear in mind the dynamic tendencies in such areas (Adams, '02, *a*, p. 126). Nor is this limited to climatic and topographic influences alone; it includes organic factors as well. It is also necessary to keep such dynamic tendencies in mind when attempting to follow the relations and movements of these three belts in their Postglacial migrations.

The three belts or waves just mentioned were composed of such distinct elements and have had such varied histories that they demand separate treatment. The wanderings of these different types, since Glacial times, is likely to make the application of geographic names confusing (Fig. 1). The members of the

first zone or wave (tundral type) have spread from the Ohio valley to the Arctic sea, the members of the second wave have moved from much the same southern limit to Hudson Bay, but

FIG. 1. Showing the present location of the five biotic types and the area invaded by them in Postglacial times. The transverse lines indicates the southern margin of the last (Wisconsin) ice sheet.

the third wave, composed of the southeastern and southwestern biota, has been relatively stationary. The first two waves entered the territory they now occupy largely from the *south*, although

we usually think of them as completely boreal forms and tending southward in their dispersal. Turning now to a brief consideration of the primary characteristics of these elements in the biota and beginning with the one which invaded the glaciated region first we have the following order of succession :

First Wave.

1. *Tundral or Barren Ground Biota.* — This element of the return movement exists to-day in the north beyond the tree limit and as relicts farther south upon mountain summits. This is a circumpolar type and has little peculiarly American. Its original center of dispersal may have been farther south near the centers of ice accumulation, or as Dixon ('95, p. 298) has suggested in the elevated regions of the tropics. In either case it has had a very nomadic existence.

As there is reason to believe that the ice did not completely cover all the northern land some of this type flourished there, in all probability, even in Glacial times, as for example, in the Point Barrow region of Alaska, where Nelson ('87, p. 27) has noted the distinctly Siberian affinities of the biota. This factor suggests that the life of this region is an overflow perhaps in preglacial or Glacial times from unglaciated Arctic Siberia.

Migration and Dispersal Routes. — The first wave biota has apparently reached its present location by a northward Glacial and Postglacial migration, and has been supplemented by certain Glacial relicts, from Alaska in particular, as has been suggested, while in more recent times some additions have been received from Asia and Greenland as has been shown by Stejneger for the wheatear ('01, *a* and *b*). The migration route of the western birds of this species points to India by way of Alaska, and the eastern ones to Africa by way of Greenland.

Probably the latest paths followed northward were along the mountain chains, where occasionally colonies have lingered, in favorable conditions, upon mountain peaks.

Second Wave.

2. *Northeastern Biota.* — The second wave was of the biotic type now represented by the northern transcontinental coniferous

forest belt. But this belt was not homogeneous from east to west and the eastern element in this wave will be considered first. On account of its wanderings, this wave as in the case of the first cannot be geographically defined in the east as a center of dispersal, without danger of confusion. Although this biota reaches its best development at the present time, in the northeast, yet it is only a relatively late arrival in that region. For eastern North America this was the "second wave" (Adams ,'02, *b*, p. 309) to pass north after the retreating arctic climate attending the decline of the Wisconsin ice sheet. The region now occupied by this biota is an area with abundant lakes, peat bogs and a region of poor drainage. The area is covered by coniferous forests but it is of a very different type from that found in the Rocky Mountain region as has been shown by Rydberg ('00, pp. 871–873). Here the very characteristic bog plant society reaches its best development as shown by Transeau ('04). This is the region of fur-bearing animals, and there are very few reptiles and amphibians. On the west this biota swings north of the Great Plains in Canada to the Rocky Mountains and then north into the Mackenzie basin.

Migration and Dispersal Routes. — The northeastern type of biota has moved from about the latitude of the Ohio valley north to its present position. Certain elements have apparently pushed far northwest to the Rocky Mountains, to the Mackenzie basin, and even overflowed into the Yukon valley — the reverse route, in all probability, was followed by certain Asiatic forms into America. This westward and northwestward dispersal has tended perhaps to overemphasize the transcontinental distribution of these northern types and shows how the determination of faunal areas based primarily upon the present conditions tends to obscure the compositeness and diversity of origin of their constituent elements. This biota reaches its greatest southward extension along the Appalachian Mountains. Laggards of this and the barren ground type form the "boreal" islands, when surrounded by the life of the following wave. These occur not only upon mountain tops, in bogs and on sand dunes but also in certain deep lakes, where the "abyssal" fauna shows very decided northern affinities, and clearly suggests them as Glacial relicts.

3. *Western Center of Dispersal.* — In the West we recognize a second center of northward migration. It is represented by the biota of the Rocky Mountains and the Pacific coast region. Its great extent, even in Glacial times, south of the ice margin and its present occupation of the field, allows this biota to be geographically defined as the Western Center of Dispersal. In contrast with the region dominated by the eastern part of this wave the western branch occupied a high mountain country. It was a coniferous forest belt, but as has been mentioned, was of a very different type from that of the northeast. The present flora of the Rocky Mountains and the coast region is of the same general type, as shown by Coville ('93, pp. 29–31) and Rydberg ('00, p. 871), although the climatic conditions are quite different in several respects. It should also be recalled that much of the recent botanical work has been done in the Rocky Mountains near the Canadian border so that later studies in the southern Rockies may, to some degree, lessen this apparent uniformity. These facts do not favor the idea of transcontinental unity of the coniferous forests but show that the direction of geographic origin, the adaptations of the biota to mountain conditions, and proximity, are factors which must be reckoned with in understanding the Postglacial repopulation of the Northwest. The same factors also suggest that the usually accepted transcontinental distribution of the fauna may be overestimated. At least it is very evident that many of the characteristic animals of the western mountains are lacking in the relatively low eastern Appalachians. Such a relation may have been closer in the past than it is at present, as is suggested by the occurrence of the pica (*Ochotona*) in the Pleistocene of Pennsylvania, although now, in North America, it occurs only in the western mountains. There is also in the West a great increase of Asiatic types, in addition to certain native elements. The mountain goat (*Oreamnus*) and big horn (*Ovis*) are representative mountain forms of the west but lacking, even as fossils, in the east. Among some invertebrates this is also true, as for example, the butterfly genus *Parnassius*, the crawfish *Potamobius*, the west coast *Unionidæ* and certain *Arionta*-like land shells, are quite distinct from eastern types. The composition and affinities of this western biota

require much more study before its true position can be determined. In marked contrast with the northeastern biota this one has long been bounded on the south and east by an arid climate.

Migration and Dispersal Routes. — With the exception perhaps of Glacial relict colonies in favorable spots along the Pacific coast, and in the unglaciated parts of Alaska, the biota of the Pacific coast and Canadian Rockies must have pushed into this region primarily from two directions in Postglacial times. To a limited extent there was an overflow of the northeastern biota but the great bulk of the population came from the Rocky Mountains and Pacific coast region south of the Canadian border. Dispersal must have been carried on under great disadvantages, on account of the topographic difficulties. But this biota, on account of its proximity, and early invasion of the region, had manifest advantages over the later arrivals. That a great wave of life moved north along the mountains from this western center is very apparent from the present affinities of the life of the region extending from southern British Columbia to Alaska. The primary highways were probably the mountains themselves, and a narrow coastal strip, now largely submerged. These lines of dispersal are today migration routes for birds. Bishop ('00, p. 50) has shown that a large part of the Yukon valley birds winter in western United States, and this clearly suggests their western origin.

The extensive distribution of certain forms in northwest North America, and their occurrence as well in the northeast, has suggested the northwestern origin of such forms. From the present standpoint it seems more likely that most of these northwestern forms have been derived from the western center of dispersal from which they spread north or later overflowed into the northeast. It also seems that the northern biota in general has had a northern rather than a southern trend to its dispersal.

The Alaskan region, in addition to its Glacial relicts, was apparently repopulated in part by a northward invasion from the western center of dispersal along the mountains, by a double invasion from Asia (Stejneger) north and south of the Stanovoj Mountains, and by contributions from the northeastern biota.

It also appears that some of the mountain biota of the Canadian Rockies were driven north into unglaciated Alaska as the ice spread from the Cordilleran center of ice accumulation.

Third Wave.

4. *Southeastern Center of Dispersal.* — The region occupied by the southeastern type of biota was largely south of the territory invaded by the ice, and its biota has therefore been relatively stable in its geographic position when compared with the extensive migrations of the first and second waves. As today, during Glacial times, this biota was bounded on the west by the arid plains. This is a region of low plains and plateaus, the higher mountains within this area still retaining the second wave types as Glacial relicts. It is probable that the first wave type never reached in abundance so far south. The climate of this southeastern center is equable and there is abundant rainfall. The dense deciduous forests furnish favorable conditions for animal life. This region has not only been important as a region of preservation, but also as a center of origin. Here there is the best development of the deciduous forest and the most characteristic features of the land and fresh water shell life of North America. This has also been the center of distribution of several vertebrate types and also for certain plants. But as this center has been discussed elsewhere (Adams, '02, *a*) only brief mention will be made here of its characteristic features.

Migration and Dispersal Routes. — With the retreat of the ice this biota formed the eastern element of the third wave. It moved north and northwest behind the coniferous forest zone. But as this biota was relatively stable its center of dispersal can be definitely defined as occupying southeastern United States, east of the Great Plains. This stability therefore makes the dispersal routes of more importance than the migrations of the biota as a whole, as the spread of this biota has apparently been influenced more by the normal increase of a populated area than by a great change in the physical conditions which was such a dominant factor farther north.

The primary routes for the land forms were the Coastal Plain and its valleys, the Appalachian plateaus, and the Mississippi

and tributary valleys. For the aquatic types the Tennessee and Mississippi Rivers were the leading highways. From the upper end of the Coastal Plain a limited number of land forms pushed up the Hudson and even worked west via the Mohawk valley to the Great Lake region. From the Mississippi numerous tributary valleys were followed, the Ohio, Wabash, Illinois, and Missouri, and thus this biota radiated rapidly. It even invaded the Great Plains along eastward flowing streams, especially along the Missouri River.

The second wave types reach their most southern extension along mountains while this third wave reaches its most northern extension along valleys, not only to the north but also upon the arid plains of the northwest.

5. *The Southwestern Center of Dispersal.* — The area occupied by the southwestern biota was largely far beyond the ice margin and, like that of the southeastern, was relatively stable in its geographic position. At present this type is represented by the life of the arid southwest, including the Great Plains, the Great Basin, the central valley of California and the Mexican Plateau. It is a vast region of arid plains, desert plateaus, and mountains, subject to great climatic extremes. In spite of the severity of the conditions of life the biota is quite varied, and many kinds are abundant. Attention has already been called (Adams, '02, *b*, p. 121) to the importance of this center and too much emphasis cannot be placed upon its importance, not only as a center of distribution, but also as the region of origin of the arid North American biota. It seems equally evident that before a reliable estimate can be made of this biota it must be carefully compared with that of the arid regions of South America and of Asia. The life of the first and second waves in the Postglacial migrations contained many forms not peculiarly American, but the southeastern and southwestern elements of the third wave show much more individuality. The southeastern center has certain endemic elements in its flora and fauna, yet several other types have their affinities duplicated in eastern Asia, and thus its individuality is somewhat lessened. On the other hand the southwestern center, although it shows some Asiatic duplication, does not appear to be so marked. So far as known to me no one has

made a detailed comparison of the arid types of the two continents.

The distinctness of the southeastern and the southwestern centers is frequently overlooked or confused. And this is especially liable to be the case when allowance is not made for the influence of local conditions upon the occurrence of certain southwestern types which have overflowed into the eastern center. This brings up the following question, which as will be seen later on, clearly emphasizes the importance of habitat study in geographical distribution. In estimating biotic areas, how much weight should be given to the occurrence of forms dependent upon limited local conditions? A bare census gives no idea of the relative weight of the units recorded or the degree of representativeness of them. The importance of such a study in a proper estimate of local conditions has been suggested repeatedly in attempting to determine the relations of these two centers. These relations have suggested that perhaps biotic affinities can be more easily and safely determined by habitat and biotic associations than primarily upon a faunistic or floristic basis. This would mean that the ecological relations rather than the taxonomic affinities should receive greater attention than is customary. It should be noted, however, that this view does not in any way belittle the importance of taxonomic work in distributional studies. But it is sufficient, at this place, simply to call attention to the ecological aspect of the subject.

But to return to the consideration of the southwest, the vegetation of this arid region is composed of grasses on the plains, and cacti, agave, yucca, and many other types of desert vegetation in the more arid places. Reference need only be made to the recent paper of Coville and MacDougal ('03) for the characteristic features and the literature on this flora. The fauna is equally peculiar and interesting. This is the region where prairie dogs, spermophiles, pocket gophers, pocket mice, wood rats, kangaroo rats are so characteristic, and the horned toads, rattlesnakes and many other reptiles reach their greatest variety and center of abundance. This has been the center for many other forms as well. Certain crawfishes (Ortmann, '02) have originated here. Many groups of insects are also characteristic. The bees of the genus

Perdita are very abundant, and as Prof. T. D. A. Cockerell informs me, are very characteristic, only a few species occurring east of the Great Plains (Cockerell, '98). The beetles of the family *Tenebrionidæ* are quite abundant. The ant-lions, *Myrmeleonidæ*, here reach their greatest development in variety and abundance. The fish fauna is limited and peculiar ; those of the Rio Grande have Mississippi River affinities, while those of the Colorado River show much endemism, as shown by Meek ('03). Of its 32 species, only 10 are known to occur elsewhere.

Migration and Dispersal Routes. — As only a small part of this southwestern center was invaded by the Glacial ice its geographic position has been relatively stationary. Since the Ice Age, however, there has been considerable overflow to the north. Starting in the southwest this biota has been spread northward along each side of the Rocky Mountains, and has invaded an arid region, a condition to which it was evidently well adapted. Even glaciated portions of British America were reached on each side of the mountains by these hardy forms of life.

Other plants and animals have spread from here into the southeast, where on account of its varied conditions of life they have been able to flourish. This, for example, is seen in the case of yucca, lizards, and pocket gophers. These forms have been able to find favorable arid *local* conditions in the southeast, as in the pine barrens and on dry hillsides, etc.

These arid types find their eastern extensions upon the dry uplands interdigitating with the southeastern types which frequent the moist valleys. They reach their extreme eastern extension, in abundance and in association, upon the prairies of Wisconsin, Illinois, and northern Indiana. But with the clearing away of the forests this eastward advance has been greatly hastened.

The aquatic life of this center has communicated with the Mississippi River, as shown by the Rio Grande fish fauna, but that of the Colorado River has been isolated to an exceptional degree, and has developed a remarkable individuality.

3. Some Factors in Biotic Interpretation.

In a previous paper (Adams, '01) the writer has discussed the relation of the baseleveling processes upon habitat differentiation

and their influence upon the successional relation of the faunas correlated with the degree of topographic development of a region. Although the fauna was mentioned in particular, these factors influence the entire biota in a similar manner. During the process of degradation of the land there is a definite and orderly succession of conditions through which the habitats pass; the brooks become larger streams, the lakes and ponds become drained, and the uplands are lowered, etc. Not only does the location of the habitats change but also their relative positions and extent. On account of the great influence which topographic conditions have upon habitats it is possible to find very diverse biotic conditions even in a relatively small area. Students of local faunas and floras frequently comment upon this diversity, and although these facts are often noted, yet but little attention is given to them because of their seeming chaos. This apparent mixture or confusion is often due to a total disregard of the habitats and the associations of the forms in them. That this occurrence is, as a rule, quite definite and orderly, may be seen by reference to the example of certain southeastern types evidently of western or southwestern origin, the yuccas and pocket gophers. These are types from an arid region, and it is important to note that when they invade a moist region they occupy the relatively dry situations — the pine barrens, sandy or rocky places — for such are the conditions most nearly approaching their original home. Such colonies form "islands" of arid types surrounded by those correlated with greater moisture. The significant fact here is the definiteness of the conditions in which they occur. Again this same tendency is shown in the extreme northward extension of the southeastern biota along protected valleys, and even far out upon the Great Plains. Similarly in southern Michigan, certain characteristic members of the southeastern biota enter the state at the southeastern and southwestern corners, rather than along the southern border, because valley highways enter the state at these corners. Apparently this same route into southeastern Michigan has been utilized by certain forest trees, insects, birds and doubtless other southern types, which have also invaded extreme southwestern Ontario. Such facts might be indefinitely multiplied, but these clearly show that

invading *elements tend to enter a region, not only at a definite place, but also tend to remain in definite habitat associations and conditions even after having once entered a region.* This habitat individuality causes more or less isolation of the various elements invading a region and furnishes an index to their direction of origin, and at the same time reinforces the idea of the regularity of their field relations. To be sure this definiteness becomes more or less blurred and indefinite along tension lines, but it is not confusing when considered with the proper perspective.

It is quite evident that the kinds of biota frequenting similar habitats must be largely different in distinct biotic regions. This may be seen by a comparison of the same habitats in regions occupied by distinct biotic types. Thus if a comparison is made between the shell life frequenting the margin of an isolated pond in Michigan and that occupying the similar habitat of a sink hole pond in east Tennessee, a marked dissimilarity is noticed. In the northern pond there will be an abundance of shells belonging to the genera *Limnæa* and *Physa*, while in the southern one these genera will be poorly represented or entirely absent. If a similar comparison is made between the shells found in rapidly flowing brooks, from the same regions, the southern stream will abound in shells of the family Pleuroceridæ, a family poorly represented in the north. The Limnæidæ are northern in their distribution, and the Pleuroceridæ are characteristically southeastern. The same general relations hold for the vegetation; in the southeast there is the deciduous forest and in the northeast a coniferous one.

On account of the unique character of the life occupying the same kind of habitats in distinct biotic regions, there results, in these regions, a different succession of forms attending changes in the topography, climate or any other factors which may influence habitats. *Thus the succession of ecological associations is likely to be similar, even in very distinct regions when similar processes and conditions are at work, yet the biotic components, the families, genera or species, etc., are likely to be quite different.* Such relations as these mean that from very diverse kinds of life there tends to be formed, *de novo* or by association, certain ecological types which become correlated with certain habitats.

Thus certain habitat types have originated many times independently. For example, the fresh water fauna was not formed all at once. This environment has been independently and repeatedly invaded by very diverse animals and from diverse habitats. The same is equally true of the minor fresh water habitats, such as that of the littoral zone or the rapid water of a brook, etc. The same is equally true of land habitats, such as caves, deserts and many other situations whose biota has been derived from all possible directions. It is thus evident that there are two fairly distinct classes of succession in a given biotic region, the adaptational one, in which the ecological aspect is prominent, and the hereditary one, in which the taxonomic or hereditary aspect receives emphasis.

From the above considerations of habitats and their biota, their successional relations and their convergent habitat and ecological tendencies, we are led to a very natural question: What is their bearing upon migration and dispersal centers? This relation is very close and unfortunately only too often completely overlooked. If in the study of the life of a given region practical recognition can be made of the above mentioned relations, which are involved in the study of the origin of the biota of given habitats, there will result a very desirable *geographic perspective*. Such a perspective will greatly aid in the determination of the relative influence of the factors of the environment. As the habitats of many plants and animals change with geographic range it is very desirable to take advantage of this variation in estimating the relative influence of different elements in the environment. In this way we may hope to distinguish between the local and geographic conditions, influences which are easily confused. It is primarily their reflex effect upon geographic distribution, and especially upon biotic interpretation which interests us at this time, a subject which can not be separated from a consideration of the relative influence of environmental factors. Habitat studies not only throw important light upon geographic origin of biotic elements but also upon the conditions of life determining routes of dispersal, and these are often very important elements in biotic interpretation. For it seems at present that it is along this line that we may expect, in the near future, some of the most rapid advances in distributional problems.

4. Summary and Conclusion.

In summarizing we may note that recent advances made in the study of the extratropical North American fauna and flora have been primarily due to the rapid accumulation of data. In the near future, rapid advances along the line of explanation and interpretation of these facts may be expected. As the present distribution is in part an *effect* it is therefore necessary to take into account certain past conditions. Very important among these factors have been Glacial and Postglacial influences upon this region. These geological changes have had a great influence on the biota, not only on account of the wonderful changes in the physical conditions of life, attending the decline of the Ice Age, but also on account of the definiteness given to the dynamic tendencies by this environment. When attempting to determine the affinities and interrelations of the present biota too much emphasis cannot be placed upon this definite dynamic tendency, and to the sources and routes followed by the life on its return to the glaciated region. This returning biota followed, in all probability, a definite successional relation and was composed of three general belts or "waves," concentrically distributed south of the ice margin. The first one was of the barren ground type, the second was represented by distinct eastern and western coniferous forest types, and the third by the biota of the southeastern and southwestern states. The first wave was of a transcontinental extent, the second while coniferous and transcontinental was composed of two distinct types, the eastern, represented by the biota of northeastern North America, and the western by that of the Rocky Mountains and the Pacific coast. The northeastern biota overflowed to the north, to the northwest into the Mackenzie basin and even a few forms into the Yukon valley and to the Rocky Mountains. The northwestern biota spread from the Rocky Mountains and Pacific coast regions in the United States north to British Columbia and Alaska. The third wave spread from the southeastern center of dispersal northward to the conifers, and west to the Great Plains. From the southwestern center the life spread north on each side of the Rocky Mountains into Canada, and only stragglers spread eastward into the humid southeast.

Further light is to be thrown upon the interpretation of these centers of dispersal and their biotic types by taking into account the successional relation of the biota, as correlated with changes of the environment. The habitat relations of organisms show that they do not occur promiscuously mixed, even within a small area, but that their relations are orderly and definite. In addition to the general successional relation attending changes of the environment, attention is called to the different kinds of organisms in different biotic regions, which make up this succession. This habitat uniqueness of the biota in different regions favors the independent formation or association of similar habitat types from very diverse kinds of biota.

With these sources of Postglacial supply, their routes of dispersal, and their definite habitat relations fresh in mind, it becomes very evident that these factors must greatly influence our interpretation of life areas. These facts strongly suggest that the present conditions of life cannot be expected to fully explain the present distribution, and clearly emphasize that the historical factor must be dynamically considered.

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